



## **Modelling the effects of climate change, species interactions and fisheries - towards Ecosystem-based Fisheries Management in the Central Baltic Sea**

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# Modelling the effects of climate change, species interactions and fisheries – towards Ecosystem-based Fisheries Management in the Central Baltic Sea.

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Ph.D. Thesis  
2010



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# **Modelling the effects of climate change, species interactions and fisheries – towards Ecosystem-based Fisheries Management in the Central Baltic Sea.**

**Martin Lindegren**

## **Academic dissertation**

By due permission of the Faculty of Science, University of Copenhagen, Denmark to be defended at Riddersalen, Charlottenlund Castle (DTU-Aqua) on Friday the 5<sup>th</sup> of February, 2010, at 09.00.

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## **Abstract**

Marine ecosystem and the services which they supply are under threat from a wide range of human activities. In order to achieve sustainability, an ecosystem-based approach to fisheries management (EBFM), i.e., integrating multiple drivers in a common framework is therefore needed. The overarching aim of this thesis is to develop a decision-support tool fit for achieving EBFM in the Central Baltic Sea, an ecosystem heavily impacted by overfishing and climate change. To that end, a theoretical approach for modelling multi-species population dynamics was combined with advanced statistical methods in order to develop a stochastic food-web model integrating species interactions, between cod and the forage fish species herring and sprat, with external forcing through commercial fishing, zooplankton and climate effects. Furthermore, by linking models across sectors, i.e., with climate and bio-economical models, we were able to account for management consequences over a wide range of policy objectives and define overall ecologically and economically optimal management solutions. To that end, our coupled modelling tool demonstrates how by adopting an ecosystem approach we may quantitatively forecast the response of Baltic fish stocks to climate change and take appropriate management actions to mitigate negative effects on future fisheries production. Furthermore, by presenting the ecological need and economic advantage of our ecosystem-based approach we may establish the institutional and political will necessary for successful implementation of EBFM in the Baltic Sea, a vital first step towards achieving long-term sustainability in marine fisheries worldwide.



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## Summary

Marine ecosystem and the services which they supply are under threat from a wide range of human activities, including overfishing, climate change and indirect alterations in species interactions. The dramatic collapses of Atlantic cod stocks illustrate clearly the failure of past management efforts and the need for developing new practises. In order to achieve sustainable marine development, an ecosystem approach to management, i.e., integrating multiple drivers in a common framework is therefore needed, but presently lacking due mainly to methodological shortcomings. The overarching aim of this thesis is to develop a decision-support tool fit for ecosystem-based fisheries management (EBFM) in the Central Baltic Sea, an ecosystem heavily impacted by human exploitation.

In the late 1980s, the Central Baltic Sea underwent large-scale alterations in the structure and functioning of the ecosystem. This so-called regime shift was likely caused by overfishing and changes in the physical environment (i.e., temperature, salinity and oxygen conditions), eventually influencing the entire food-web dynamics from primary producers to top-predators. The recognition of the ecosystem context therefore calls for the integration of both external and internal drivers in model development. To that end, a theoretical approach for modelling multi-species population dynamics was combined with advanced statistical methods in order to develop a food-web model integrating species interactions, between cod and the prey species herring and sprat, with external forcing through commercial fishing, zooplankton and climate effects on the Central Baltic ecosystem. Furthermore, by linking models across sectors of interest, i.e., including ecological, climate and bio-economical models, we were able to account for management consequences over a wide range of objectives and define overall optimal management solutions.

Based on the derived patterns of species interactions and the external forcing through fishing, zooplankton and climate, our food-web model clearly recreates and explains the past variability in Central Baltic fish stocks. As such, the so-called “gadoid outburst” (i.e., the strong and synchronous increase in several Atlantic cod stocks during the late 1970s) of Baltic cod could be explained by a period of historically low exploitation in combination with record high salinities, enabling successful reproduction due to high egg and larvae survival in the entire Baltic Sea.

Furthermore, we used our coupled climate-food-web model to explore whether given the present knowledge on climate effects, fishing and species interactions, we in hindsight could have managed the Baltic cod stock in ways such as to avoid the collapse. To that end, we formulated an adaptive management strategy in setting precautionary exploitation levels. By adapting fishing pressure to climate conditions and species interactions, our simulations show that we could indeed have prevented the cod stock from collapsing and promoted a recovery above ecologically safe levels.

In an effort to adopt a holistic management perspective, we finally coupled the food-web model to a simple bio-economic model aiming to compare revenues of the Baltic cod fishery across management strategies. Based on our results, we argue that our adaptive management strategy would not only be ecologically but economically profitable due to increased landings and reduced fishing costs as the stock and hence the catchability is allowed to increase. These results support the importance of investing in “natural capital” (i.e., in future stock size) as a long-term management strategy for the Baltic cod.

In summary, by improving the methodological development towards increasing ecological realism in fisheries modelling and providing cross-disciplinary exchange of scientific concepts and ideas, this Ph.D. contributes to the implementation of regionalised ecosystem-based management in the Central Baltic Sea, a vital first step towards achieving long-term sustainability in marine fisheries worldwide.



## Resumé

Marine økosystemer og de goder, de leverer, er truet af en bred vifte af menneskelige aktiviteter, herunder overfiskning, klimaforandringer og indirekte ændringer i samspillet mellem arterne. Det dramatiske sammenbrud af Atlanterhavets torskebestandene påviser klart tidligere tiders fejlslagne forvaltning og behovet for at udvikle ny praksis. For at opnå en bæredygtig marine udvikling, er en økosystembaseret forvaltning (dvs. integration af flere samspillene faktorer i en fælles ramme) nødvendigt, men i øjeblikket fraværende på grund af især metodologiske mangler. Det overordnede mål med denne afhandling er at udvikle et operativt værktøj egnet til rådgivning af en økosystembaseret og bæredygtig fiskeriforvaltning (EBFM) i den centrale del af Østersøen, et økosystem, stærkt påvirket af menneskelig udnyttelse.

I slutningen af 1980'erne gennemgik den centrale Østersø store ændringer i struktur og funktion af økosystemet. Denne tilstandsændring, der kan opfattes som et slags regimeskifte, var sandsynligvis forårsaget af overfiskning og ændringer i det fysiske miljø (dvs. temperatur, saltholdighed og iltindhold), som i sidste ende påvirkede hele fødenettet fra primærproducenter til toppredatorer. Erkendelsen af økosystemets sammenhængende måde at virke på, opfordrer derfor til integration af både eksterne og interne faktorer i en model udvikling. Med henblik herpå kombineredes en teoretisk populationsdynamisk model med avancerede statistiske metoder. Herved blev det muligt at udvikle en fødenetmodel for den centrale Østersø der integrerer samspillet mellem arterne, mellem torsk og byttedyr sild og brisling, med eksterne faktorer som kommerciel fiskeri, dyreplankton og klima virkninger. Desuden, ved at koble modeller på tværs af interesser og fagområder, herunder økologiske, klimatiske og bio-økonomiske modeller, blev det muligt at redegøre for forvaltningen konsekvenser over en bred vifte af mål og definere de overordnede optimale løsninger.

Baseret på de afledte mønstre i samspillet mellem arterne og de ydre faktorer gennem fiskeri, dyreplankton og klima, har fødenetmodellen været i stand til at genskabe og forklare den tidligere variation i fiskebestande i Østersøen. Som sådan, kan den såkaldte "gadoid outburst" (dvs. de stærke og synkrone stigning i flere Atlanterhavs torskebestandene, herunder Østersøen i slutningen af 1970'erne) for Østersøens

vedkommende forklares ved en periode med historisk lav fiskeritryk i kombination med rekordhøje saltholdigheder, der betinger en succesfuld reproduktion i hele Østersøen i sær på grund af en høj æg- og larveoverlevelse. Endvidere er den koblede klima-fødenet model brugt til at undersøge, om man i lyset af den nuværende viden om klimaeffekter, fiskeri og samspillet mellem arterne, i bakspejlet kunne have undgået sammenbrud af torskebestanden i Østersøen. Til dette formål formuleres en adaptiv forvaltning strategi for fastsættelse af præventive udnyttelsesniveauer. Ved at tilpasse fiskeritrykket til klimaforhold og samspillet mellem arterne, viste simulationer, at vi faktisk kunne have forhindret et sammenbrud af torskebestanden ved at sikre en bestand over økologisk sikkert niveau.

Endelig, i et forsøg på at indføre et mere sammenhængende og holistisk forvaltningsperspektiv, er fødenetmodellen koblet til en simpel bio-økonomisk model, der sigter mod at sammenligne indtægterne for torskefiskeriet i Østersøen på tværs af forvaltningsstrategier. Baseret på disse resultater, hævdes det at en mere adaptive forvaltning strategi ikke kun vil være økologisk forsvarlig, men økonomisk rentabel som følge af øgede landinger og reduceret. Disse resultater understøtter vigtigheden af at investere i "naturlige kapital" (dvs. sikring af fremtiden bestandsstørrelse) som en langsigtet forvaltningsstrategi for torsk i Østersøen.

Sammenfattende ved at forbedre den metodologiske udvikling i retning af stigende inddragelse af en økologisk realisme i fiskerimodellering og udbygning af tværfaglig udveksling af videnskabelige begreber og ideer, er det mit håb at denne Ph. D. kan bidrage til en mere regionspecifik og økosystembaseret forvaltning i den centrale del af Østersøen. Dette kunne være et vigtigt første skridt hen imod at opnå langsigtet bæredygtighed i havfiskeri i fremtiden.

## **List of original publications**

This dissertation is based on the following four papers, referred throughout the text by their Roman numerals:

I. Lindegren M, Möllmann C, Nielsen A, Stenseth N. C. (2009) Preventing the Collapse of the Baltic Cod Stock through an Ecosystem-based management approach. Proceedings of the National Academy of Sciences of the United States of America 106:14722-14727.

II. Lindegren M, Möllmann C, Nielsen A, Brander K, MacKenzie B, Stenseth N. C. Ecological Forecasting under Climate Change – the case of Baltic cod. Proceedings of the Royal Society B-Biological Sciences (*in revision*)

III. Lindegren M, Möllmann C, Hansson L. A. Biomanipulation - a tool in Marine Ecosystem Management and Restoration? Ecological Applications (*in revision*)

IV. Lindegren M, Diekmann R, Möllmann C. Regime shifts, Resilience and Recovery of a Local Cod Stock. Marine Ecological Progress Series (*in press*)

## **1. Introduction and background**

Marine ecosystems are in a rapid state of deterioration, as evidenced by the poor conditions of commercially important fish stocks worldwide (Hutchings & Reynolds 2004; Worm et al., 2009). Whether caused by overfishing (Myers et al., 1997; Jackson et al., 2001), climate change (Beaugrand et al., 2003; Lilly et al., 2008) or a combination of several factors (Ottersen et al., 2006; Anderson et al., 2008) policy makers, managers and the general public are rightly concerned that marine ecosystem and the services which they supply are under threat from a wide range of human activities. In order to achieve future ecological and economical sustainability, a new holistic paradigm for managing marine resources is therefore needed (Hilborn 2007). To that end, an ecosystem approach has been adopted as the fundamental principle for sustainable marine management regionally (i.e., within EU) and internationally (FAO 2003; EC 2009). Though several definitions exist, all of these can be considered as expressions of integrated measures that, to varying degrees, are embracing the concept of ecosystem-based management (UNEP 2006). While spatial scales and issues addressed differ between areas and ecosystems, the fundamental principles: (i) integrates ecological, social, and economic goals; (ii) recognize humans as key components of the ecosystem; (iii) incorporates understanding of ecosystem processes and how ecosystems respond to environmental perturbations; and (iv) addresses the complexity of natural processes and social systems by using an adaptive management approach in the face of uncertainty (see [www.ebmtools.org](http://www.ebmtools.org) and MacLeod et al. (2005) for details).

Ecosystem-based fisheries management (EBFM), i.e., integrating multiple drivers and services in a common fisheries management framework (Pikitch et al., 2004; Marasco et al., 2007), forms a central part of ecosystem-based marine management and focuses primarily on sustaining healthy marine ecosystems and the fisheries they support (Pikitch et al., 2004). However, despite the recent conceptual developments (Marasco et al., 2007), an EBFM-approach is far from operational, due mainly to methodological shortcomings in terms of incorporating ecological detail, representing climate effects and providing estimates of uncertainty in fisheries models (deYoung et al., 2004; Brander 2007). Hence, single-sector (species) based management practices still remain the basic means of resource exploitation in marine ecosystems worldwide.

The dramatic declines of North Atlantic cod stocks (*Gadus morhua*) provide a striking and often cited example of the failure of fisheries management during the past (Murawski et al., 1997; Hutchings 2000). These stock collapses mainly resulted from overfishing (Myers et al., 1997; Jackson et al., 2001) and climate driven declines in productivity, generally caused by hydrographic changes (e.g., temperature and salinity) and indirect alterations in food composition and abundance (i.e., zooplankton) impairing growth and survival of early life-history stages and eventually reproductive output, i.e., recruitment (Beaugrand et al., 2003; Lilly et al., 2008). In accordance with this, the recruitment failure of Eastern Baltic cod was mainly caused by high egg and larval mortalities due to climate-induced hydrographic changes in salinity and oxygen conditions in the Central Baltic Sea (Köster et al., 2005; Möllmann et al., 2008). In several areas the collapse of cod stocks was part of or one of the major factors inducing large-scale reorganization of ecosystems (Frank et al. 2005, Möllmann et al., 2009). These so-called ecosystem regime shifts are frequently caused by climatic changes (Hare & Mantua 2000, Scheffer et al., 2001) and/or by overexploitation resulting in cascading trophic interactions (Frank et al., 2005; Scheffer et al., 2005). Similarly to other areas, the Central Baltic Sea underwent both regime shifts and trophic cascades (Casini et al., 2008; Möllmann et al., 2009). Such alterations in ecosystem structure typically affect species interactions, eventually influencing food-web dynamics through both positive and negative feedback loops (Ives 1995). The recognition of the ecosystem context in the collapse of fish stocks calls for the integration of external and internal drivers, e.g., commercial fishing, climate change and species interaction, in the development and implementation of ecosystem-based modelling tools fit for achieving sustainable development within the framework of EBFM.

## **2. Motivation and objectives of the study**

The overarching aim of this thesis is to develop an ecosystem-based modelling tool capable of incorporating the effects of climate change, species interactions and fisheries in a common EBFM framework for the Central Baltic ecosystem. To that end, a theoretical approach for modelling multi-species population dynamics (Ives 1995; Ives et al., 2003; Ripa & Ives 2003) was combined with advanced statistical methods (Harvey 1989) in order to develop a stochastic food-web model integrating species interactions, between cod and the forage fish species herring (*Clupea harengus*) and sprat (*Sprattus sprattus*), with

external forcing through commercial fishing, zooplankton and climate effects on the Central Baltic ecosystem. The model development undertaken has proceeded in three major working steps, each representing a specific objective of this Ph.D. study:

- i) Explaining and recreating (i.e., hindcasting) the historical variability in spawning stock biomass (SSB) of Central Baltic cod, herring and sprat based on the observed patterns of climate variability and fisheries exploitation from 1974-2004.
- ii) Model coupling with regionally downscaled climate models (Meier 2006; Meier et al., 2006) and bio-economic models (Döring and Egelkraut 2008) into a fully dynamic cross-disciplinary EBFM tool for the Central Baltic Sea.
- iii) Scenario testing and quantitative risk assessments for future fisheries production under different climate and fisheries management scenarios in order to provide scientific advice for achieving sustainable fisheries management in the Central Baltic Sea.

By improving the methodological development towards increasing ecological realism in fisheries modelling and providing cross-disciplinary exchange of scientific concepts and ideas (e.g., with climatologists, oceanographers and bio-economists), this Ph.D. contributes to the implementation of regionalised ecosystem-based management in the Central Baltic Sea and beyond.

### **3. The Central Baltic Sea – an overview of Ecosystem characteristics**

The Baltic Sea is a large semi-enclosed sea separated from the North Sea by a number of narrow straits and shallow sills (Fig. 1). Due to its brackish conditions and relatively short geological history (~11 000 years), the Baltic Sea ecosystem is characterized by low species diversity, as only few species have been able to adapt, or had time to evolve to tolerate the environmental conditions. Consequently, the fish community of the open Baltic Sea is almost entirely dominated by only three species, the demersal predator cod and the planktivorous prey species sprat and herring (i.e., together accounting for ~ 85% of total fish biomass). Furthermore, these fish species represent the commercially most important fisheries resources, followed by relatively limited landings of e.g., salmon (*Salmo salar*) and flounder (*Platichthys flesus*).

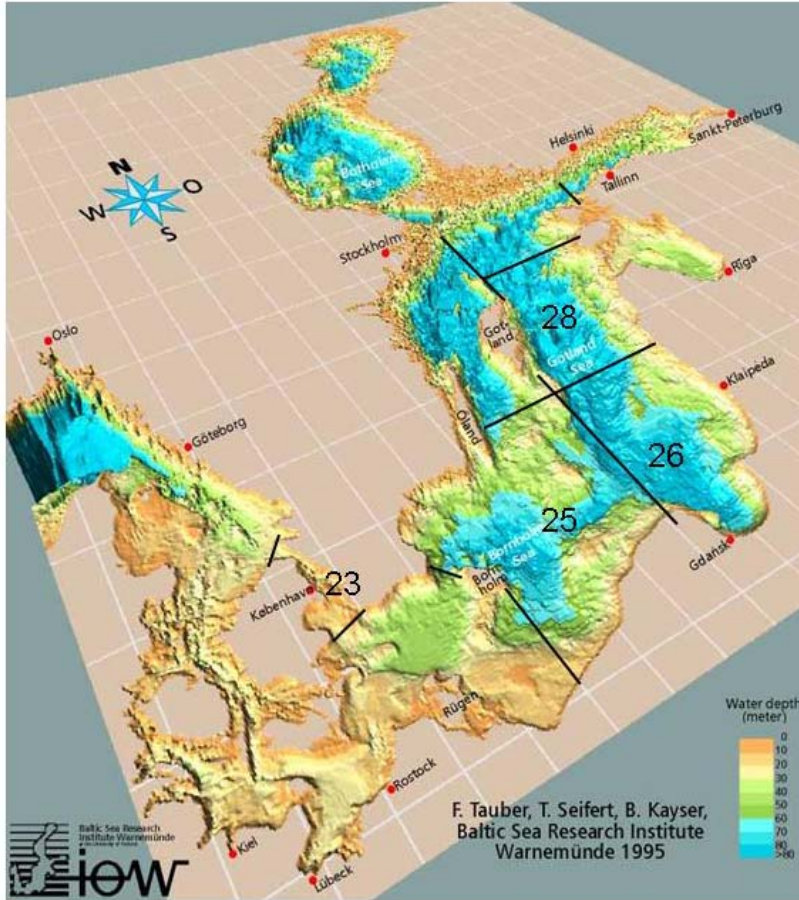


Fig. 1. A bathymetric map of the Baltic Sea showing the locations of the main deep basins of the Central Baltic Sea (i.e., the Bornholm Basin, the Gdansk Deep and the Gotland Basin) and the division into ICES Subdivisions.

The central part of the Baltic Sea (referred throughout the text as the Central Baltic Sea) encompasses three deep basins (Fig. 1), the Bornholm Basin, the Gdansk Deep and the Gotland Basin, largely coinciding with the geographical assessment areas (i.e., Subdivisions) 25, 26 and 28 as defined by *the International Committee for Explorations of the Seas* (ICES). These basins form important areas for spawning, recruitment and growth of Baltic fish populations. Characteristic to the hydrography of these basins is a permanent halocline separating low salinity surface waters from high saline deep waters (i.e., at ~70-100 meters). Deepwater conditions can only be enhanced by inflows of saline and oxygenated water from the North Sea (Matthäus & Franck 1992). A lack or low frequency of these events, as has been observed during the past decades (Fig. 2a), leads to low salinity (Fig. 2b) and oxygen levels (Fig. 2a) and hence to detrimental reproductive conditions for e.g., cod (Köster et al., 2005). Additionally, the Baltic Sea is heavily influenced by nutrient inputs from agriculture and industrial activities (by more than 85 million people inhabiting nine different countries within the catchment area), which by increasing oxygen

consumption rates in the deep basins further increase the spread of bottom anoxia. As a result of anthropogenic impact the Baltic Sea is presently considered in a eutrophied state as compared to the 1950s and before (Österblom et al., 2007).

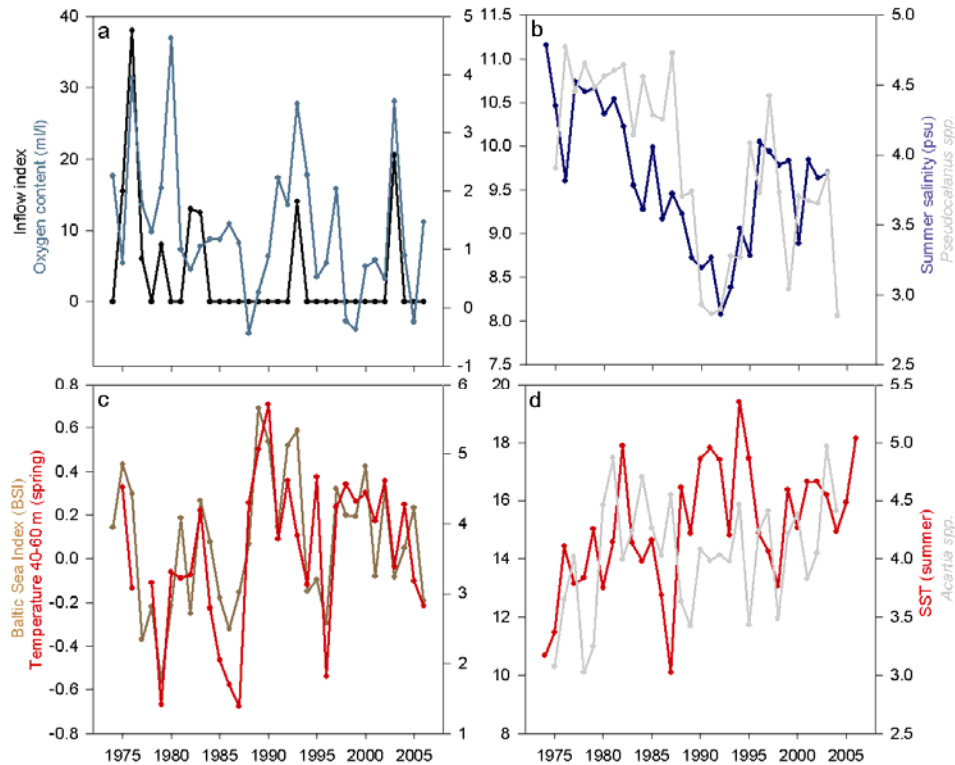


Fig. 2. Hydrographic conditions in the Central Baltic Sea from 1974 to 2007. In (a) the inflow index, reflecting the frequency and magnitude of Baltic inflow events from the North Sea, is plotted together with deep water oxygen conditions in the Bornholm basin. In (b) summer deep water salinity and abundance of the copepod species *Pseudocalanus* spp. in the Gotland Basin are shown. In the lower panels (c, d), the relationship between the winter Baltic Sea Index (BSI) and spring temperature, as well as the synchrony between summer SST and abundance of the warm water copepod species *Acartia* spp. in the Gotland Basin are plotted.

Changing hydrographic conditions since the late 1980s have significantly altered the living conditions for animal populations inhabiting the area (Fig. 2). The main trends are lowered salinity and oxygen levels due to low inflow frequency and increased temperatures (Möllmann et al., 2009). Partly due to these changes, the Central Baltic ecosystem shifted rapidly from a cod dominated to a sprat dominated ecosystem state in the early 1990s (Köster et al., 2003; Möllmann et al., 2008). This ecosystem regime shift was likely



triggered by coinciding overfishing and recruitment failure of cod due to low salinities and hypoxia (Köster et al., 2005; Möllmann et al., 2008). The climate effect works directly on egg survival (Nissling 2004), but as well indirectly on the availability of the copepod *Pseudocalanus acuspes* (Hinrichsen et al., 2002), the main food source for larval cod. Following the collapse of the cod stock, sprat was released from predation (Köster et al., 2003; Möllmann et al., 2008). In combination with temperature driven recruitment success (MacKenzie & Köster 2004) the stock increased to record high levels. The large sprat stock may presently inflict key negative feedbacks by preying on cod eggs (Köster & Möllmann 2000) and reducing the main food source for cod larvae and herring (i.e., *Pseudocalanus acuspes*; Möllmann & Köster 2002; Voss et al., 2003), thus maintaining the ecosystem in its currently less desirable ecosystem state (Bakun & Weeks 2006; Möllmann et al., 2008).

## **4. Background of material, methods and modelling approaches**

### *4.1 Data requirements*

Since this Ph.D. project relies on a broad spectrum of time-series data covering all aspects of the structure and functioning of the Central Baltic Sea ecosystem (i.e., from abiotic to biotic variables at multiple trophic levels), already existing monitoring data was collected from various sources around the Baltic Sea. A major vehicle for data collection and ecosystem analysis has been the *Working Group on Integrated Assessments of the Baltic Sea* (WGIAB), hosted by ICES and the *Helsinki Commission* (HELCOM), where an extensive database for several sub-systems of the Baltic Sea has been compiled, quality controlled and updated on an annual basis (WGIAB 2008). This data involve e.g., fish-stock assessment outputs from ICES, lower-trophic level assessment data from HELCOM, zooplankton data from the *Latvian Fish Resources Agency* (LATFRA) and hydrography data from the *Swedish Meteorological Institute* (SMHI). Other external sources not directly linked to large institutions have also been used when appropriate.

In addition to the above mentioned data sources, extensive literature reviews were conducted in order to incorporate specific regional knowledge of the structure and functioning of the Central Baltic Sea ecosystem. This knowledge constitutes a vital part in the setup, fitting and validation of the food-web model (see section 4.3-4.4) and forms the scientific basis for sound interpretation of model results and simulations.

#### *4.2 Ecosystem-based modelling*

To be valuable in decision-making and management, ecosystem-based models require a manageable degree of complexity, to incorporate ecological detail, represent environmental and fishing effects and provide estimates of uncertainty (deYoung et al., 2004). Traditional stocks assessment models still rely heavily upon single-species modelling, thus disregarding vital ecological mechanisms and indirect responses to climate change channelled through species interactions (Ives 1995). Consequently, methodologies presently in use are largely unfit to provide reliable information for decision-making within the context of EBFM and in the face of climate change. Statistical models have proven useful in incorporating key ecological and environmental drivers and evaluating multiple sources of uncertainty (Harwood & Stokes 2004; Hjermann et al., 2004), an advantage over existing multi-species models developed for the Baltic Sea, e.g., the mechanistic Stochastic Multi Species (SMS) model (ICES 1996) and the Ecopath with Ecosim mass-balance model (Harvey et al., 2003). By integrating multiple drivers and uncertainties, multivariate autoregressive models (MAR(1)) provide an important tool for EBFM (Ives 1995; Ives et al., 2003). Surprisingly, it has rarely been extended beyond theory, and its application to real food-webs (Ives et al., 1999; Hampton & Schindler 2006) has, to our knowledge, never been used in fisheries management.

Furthermore, in order to develop a holistic EBFM tool, being able to account for management consequences over a range of policy objectives, including ecological, economic and social aspects is of vital importance (Hilborn 2007). Hence, linking models across sectors of interest in an end-to-end perspective is needed (deYoung et al., 2004). Our coupled EBFM-toolbox, including ecological (section 4.4), climate (section 4.5) and bio-economical models (section 4.6) will enable us to respond to, and seek to reduce conflicts between policy objectives by finding optimal management solutions across sectors (Hilborn 2007). All analysis described in the following sections were conducted using the R ([www.r-project.org](http://www.r-project.org)) and Brodgar software ([www.brodgar.com](http://www.brodgar.com)).

#### *4.3 Multivariate Autoregressive models (MAR)*

First-order multivariate autoregressive models (MAR(1)) provide a statistical framework for modelling species interactions at multiple trophic levels (Ives et al., 2003) and

essentially functions as a set of lagged multiple linear regression equations (one for each species ( $n$ ) of the food-web) solved simultaneously to arrive at the most parsimonious model overall (Hampton & Schindler 2006). Written in state-space form, a MAR(1) model is given by:

$$\mathbf{X}(t) = \mathbf{B}\mathbf{X}(t-1) + \mathbf{C}\mathbf{U}(t-y) + \mathbf{E}(t) \quad (1)$$

$$\mathbf{Y}(t) = \mathbf{Z}\mathbf{X}(t) + \mathbf{V}(t) \quad (2)$$

where  $\mathbf{X}$  is a vector of species abundances at time  $t$  and  $t-1$  respectively, and  $\mathbf{B}$  is a  $n \times n$  parameter matrix of pair-wise species interaction terms, hence an analogue of the “community matrix” developed in food-web theory by May (1972) and Pimm (1982). The covariate vector  $\mathbf{U}$  contains values of ( $p$ ) covariates known to affect reproduction, growth and survival of each species respectively. These covariates may include both biotic and abiotic variables and should be selected based on existing knowledge on the ecology of the species. Furthermore, lagged variables ( $t-y$ ) may be introduced in order to reflect potential time-delayed effects of covariates on species abundances, such as may be expected when covariates affect primarily early-life history stages. Consequently,  $\mathbf{C}$  is a  $n \times p$  matrix of parameters specifying the effect of covariates on each species. The process error  $\mathbf{E}(t)$  is assumed multivariate normal and temporally uncorrelated. Likewise, the observation error of the covariance matrix of the normal random variable  $\mathbf{V}(t)$  is assumed independent. Regression parameters (i.e., in  $\mathbf{B}$  and  $\mathbf{C}$ ) are found by maximum likelihood estimation using a Kalman filter (Harvey 1989). The Kalman filter is a recursive estimator that sequentially calculates the unobserved values  $\mathbf{X}(t)$  from the previous time step ( $t-1$ ) using the model formula specified in Eq. 1. Predictions from the so-called “hidden” state are then updated using the observed values,  $\mathbf{Y}(t)$  of the “true” state (Eq. 2).

#### *4.4 The BALMAR food-web model – fitting and selection*

In fitting the Baltic Sea MAR(1) food-web model (BALMAR), we used time-series data on spawning stock biomass (SSB) of cod, sprat and herring from 1974-2004 derived from multi-species stock assessment (MSVPA) in the Baltic Sea (ICES 1996). Model fitting was performed separately on both log-transformed and normalized SSB values. To include the top-down effect of commercial fishing on the dynamics of the three species, time-series on mean annual fishing mortality ( $F$ ) of cod, sprat and herring were used as covariates ( $\mathbf{U}$ ).

Furthermore, to encompass the effect of climate and zooplankton, abiotic and biotic variables known to affect recruitment of cod, sprat and herring were included. To take into account any geographical differences in hydrographic forcing (MacKenzie et al., 2007), climate variables were taken separately from the two main sub-basins of the Central Baltic Sea, the southern Bornholm Basin and the northern Gotland Basin (Fig. 1). Since egg and larval survival of Central Baltic cod is mainly affected by salinity and oxygen in these basins (Köster et al., 2005), as well as indirect effects of food availability of the copepod *Pseudocalanus acuspes* (Hinrichsen et al., 2002; Voss et al., 2003), we included salinity and oxygen concentration in the deepwater and  $\ln(x+1)$  transformed biomass of *Pseudocalanus acuspes* as potential covariates. We further used the reproductive volume, i.e., the water volume with salinity  $> 11$  psu and oxygen content  $> 2\text{ml}\cdot\text{l}^{-1}$  representing the minimal conditions for successful cod egg development in the deep Baltic basins (MacKenzie et al., 2000).

Temperature is the main environmental variable influencing sprat recruitment (Köster et al., 2003) directly affecting egg and larval survival (Nissling 2004). Indirectly temperature affects the production and hence the availability of the copepods *Acartia* spp. (Voss et al., 2003), important for the survival of larval sprat (Dickmann et al., 2007). Thus we included both temperature and  $\ln(x+1)$  transformed biomass of *Acartia* spp. as potential covariates in the analysis. Hansson et al. (2007) argue that eutrophication has a strong impact on the Baltic ecosystem, as enhanced primary production increases total fish production but at the same time may induce hypoxia in bottom waters. To account for this effect, we used  $\ln(x+1)$  transformed values of spring and summer Chl *a* in the analysis. Finally, the Baltic Sea Index (BSI) was included as it reflects the impact of climate variability on oceanographic processes in the area (Lehmann et al., 2002).

To avoid co-linearity between climate and zooplankton covariates, we included only one abiotic and biotic variable per species in the full model. Prior to model reduction the full model was therefore fitted with each covariate separately and at different time lags (1-3 years). The time lags aim to represent the period until recruitment of the species to the fisheries. The covariates included in the full model were then chosen based on the significance level of the parameters. Then by stepwise model reduction, the full model was

penalized for complexity. We minimized the negative log-likelihood function and applied the likelihood ratio test to compare full and reduced models. Variables not improving the fit of the model were thus excluded from the final model.

#### ***4.5 Regional climate modelling and forecasts for the Baltic Sea***

In order to study the effects of climate change on the Baltic Sea food-web, we based our forecasts (Fig. 3) on regional climate simulations from the BALTEX Assessment of Climate Change for the Baltic Sea Region (BACC 2007). It applies a multi-model ensemble approach (i.e., the PRUDENCE project; Christensen et al., 2007) of seven regional circulation models (RCMs), five global circulation models (GCMs), and two IPCC-emission scenarios (i.e., B2 and A2) to explore the range of outcomes and to enhance confidence in projected climate changes in the Baltic Sea region (Meier 2006; Meier et al., 2006). This approach takes into account projections for precipitation and run-off, causing a freshening (i.e., decreasing salinities) of the Baltic Sea, as well as the effect of wind-driven inflows of high-saline water from the North Sea. Since presently only the projected changes (i.e., from 2071-2100) but no transient time-series for forecasted climate conditions at different seasons, areas and depths are available (Meier 2006), we simulated future time-series representing not only the projected change but the uncertainty and variability in climate forcing during the coming 100 years. By using an AR(1) climate model (Ripa & Lundberg 1996) we generated “red-shifted” transient time series (Steele & Henderson 1984) ( $\Phi_{t+1}$ ) concerning specifically spring sea surface temperature (SST) and summer salinity (80-100m) of the Gotland Basin (i.e., the largest and northernmost spawning area of cod in the Baltic Sea):

$$\phi_{(t+1)} = \alpha\phi_{(t)} + \beta\varepsilon_{(t+1)} \quad (3)$$

where  $\varepsilon_t$  is random “white” noise (zero mean and unit variance),  $\beta$  a parameter specifying the degree of environmental variation and  $\alpha$  a measure of the degree of autocorrelation in the time series. The future series (from 2005-2104) were simulated based on the actual mean, variance and autocorrelation of the observed time series from 1974-2004. To simulate the predicted increase in Baltic Sea SST by 3.5°C and decrease in salinity by 0.8–4.8 psu, i.e., an 8-50% decrease dependent on differences between the GCMs used (Meier et al., 2006), a gradual trend in the mean over 100 consecutive years was added.

Though species may respond differently to climate over a wide range, e.g., changing from a positive to a negative response from low to high temperatures (MacKenzie et al., 2004), we assume that the responses of Baltic cod to salinity and sprat to temperature remain positive, at least within the relatively narrow intervals predicted (MacKenzie et al., 2004; Köster et al., 2005). Therefore, using these simulations as inputs, we forced our food web model bottom-up, exploring the impact of climate change on the future dynamics of Baltic cod, sprat and herring. Since herring was not directly forced by climate, but rather indirectly through its main prey, *Pseudocalanus acuspes* (Möllmann et al., 2003; Voss et al., 2003), we simulated the climate effect as an indirect linear response to salinity mediated by *Pseudocalanus acuspes* (Salinity-*Pseudocalanus acuspes*:  $r = 0.65$ ,  $n = 26$ ).

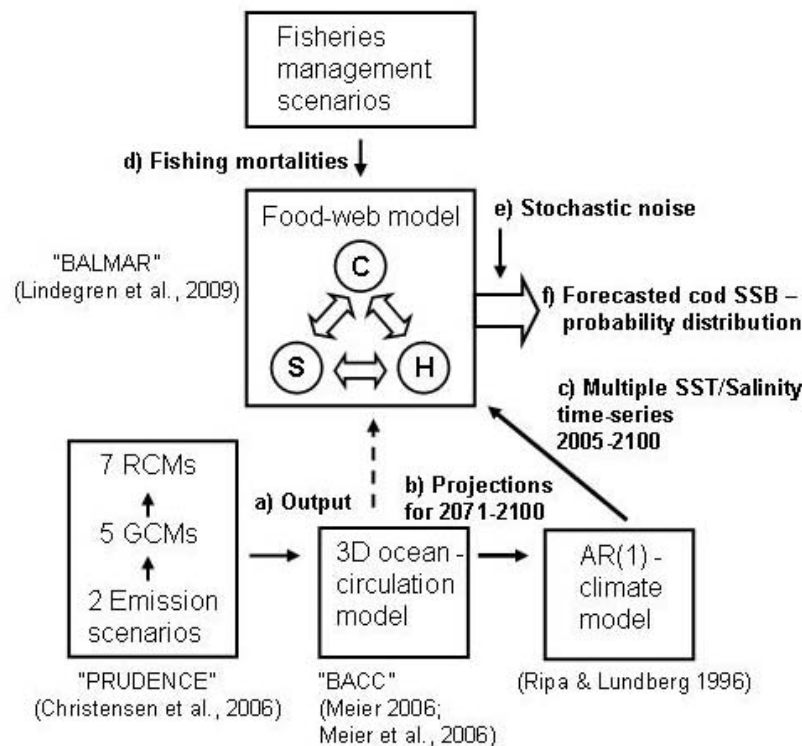


Fig. 3. A coupled food web-climate model approach to forecasting Baltic cod stock dynamics in the 21<sup>st</sup> century. (From Paper II).

#### 4.6 Bio-Economic modelling of the Baltic fishery

Calculating net present values (NPV) is a standard method for measuring the financial appraisal of long-term projects and is widely used in fisheries economics (Sumaila 2004). With both available estimates of price and fishing costs, fishery economists are able to perform cost-benefit analysis of management strategies aiming to optimize economic profit.

Using a bio-economic model for the Baltic cod fishery, Döring & Egelkraut (2008) show that a recovery program for Eastern Baltic cod is not only ecologically viable but economically profitable as fishermen will experience greater landings and revenues in the years following the recovery program. By coupling their economic model with the BALMAR food-web model, we quantified the revenue under different fisheries management scenarios. The net present value (NPV) is computed as:

$$NPV = \sum_{t=1}^T e^{-\delta t} \{p[Y_t] - c[B_t]\} Y_t \quad (4)$$

where  $\delta$  denotes the discount rate of the fishermen,  $Y(t)$  the simulated yield (i.e., landings) and  $B(t)$  the simulated stock size. Since market price depends on supply (i.e., the price decrease with yield), we consider the market price,  $p$  (€/tonne) a linear function of yield. (Regression parameters were calculated from the observed market price (adjusted for inflation rate for each year) and landings from 1974-2004). A major challenge in fisheries economics is to estimate fishing costs for a particular species. The difficulties arise from vessels generally targeting several species over different seasons but applying the same input factors (Röckmann et al., 2008). To be able to perform bio-economic evaluations of management strategies in a multi-species context, quantifying fishing costs for all targeted species is needed. However, since no reliable estimates of fishing cost are available for Baltic sprat and herring (for cod see: Eggert & Tveterås 2007, Döring & Egelkraut 2008, Röckmann et al., 2008) we calculated the NPV of future landings for the Baltic cod fishery only. The fishing costs ( $c$ ) were calculated on a fixed number of cod fishing licenses and include investments as well as running costs for the year 2004 (Döring et al., 2005). Fishing costs are assumed to decrease as stock biomass increase due to increased catchability and reduced fishing effort.

#### *4.7 Integrated Ecosystem assessment and regime shift analysis*

In parallel with the development of a coupled EBFM modelling tool (described in sections 4.4 to 4.6), integrated ecosystem assessments were carried out within WGIAB to detect and describe ecosystem regime shifts in various sub-systems of the Baltic Sea (WGIAB 2008). To that end, multivariate statistical methods, including (PCA) and Chronological Clustering (Legendre et al., 1985; Legendre & Legendre 1998) were applied in order to identify key

ecosystem drivers (i.e., top-down, bottom-up and climate control) underlying regime shifts in each sub-system specifically. My contribution to this work concerns the Sound (i.e., ICES Subdivison 23), a narrow strait situated in the interface between the North and Baltic Seas (Fig. 1). Though being hydrologically connected to the Baltic Sea by the northward flow of brackish surface water and to the North Sea by the southward flow of high-saline bottom water, the Sound differs from its neighbouring areas in terms of the magnitude of fishing pressure on the local fish stocks, a difference attributed to a trawl fishing ban since 1932 (Svedäng et al., 2004). Hence, in order to disentangle the importance of climate and fishing as drivers of regime shifts and fish stock collapses in marine ecosystems, we performed an assessment of the ecosystem development in the Sound and compared the dynamics with the neighbouring North and Baltic Seas (paper IV).

In order to characterise the Sound ecosystem and its abiotic environment, a dataset of 50 time-series (i.e., abiotic and biotic at multiple trophic levels), covering a period from 1979-2005 was selected and analysed. Firstly, PCA was used to extract the most important modes of variability in the time series. Secondly, in order to identify potential regimes in the datasets, Chronological Clustering was performed to objectively identify the years where the largest shifts occurred (Legendre et al. 1985, Legendre & Legendre 1998). In a further analysis we also applied the Sequential Regime Shift Detection Method (STARS), an algorithm designed to detect statistically significant shifts in the mean level and the magnitude of fluctuations in time-series (Rodionov 2004).

## **5. Summary of main results and findings**

### ***5.1 Food-web model diagnostics and validation***

The reliability and quality of the model development undertaken during this Ph.D. project rely largely on the methodological knowledge and the specific ecosystem insight on which we base and validate our models. This section will provide a brief insight into the validation process undertaken. To that end, a number of diagnostics were applied to assess whether the BALMAR model gave a reasonable description of the food-web dynamics. Firstly, residuals proved normally distributed and independent for all species (Lindegren et al., 2009). Secondly, both  $R^2$  values and conditional  $R^2$  values, i.e., reporting the proportion of change explained between subsequent years, show a high degree of explained variance for



all species (e.g., 95%, 89% and 98% for cod, sprat and herring respectively). Finally, a stability analysis of the final parameters of the community matrix (**B**) reveal a dominant eigenvalue below one ( $\lambda_1 = 0.91$ ), indicating a stable, stationary process (Ives et al., 2003). Our model thus has captured the essential dynamics of a natural, stable system. More importantly however, the parameters of the finally selected model captured accurately the known mechanisms of species interactions within the food-web as well as the effects of fishing, zooplankton and climate variability on the three species respectively (Fig. 4).

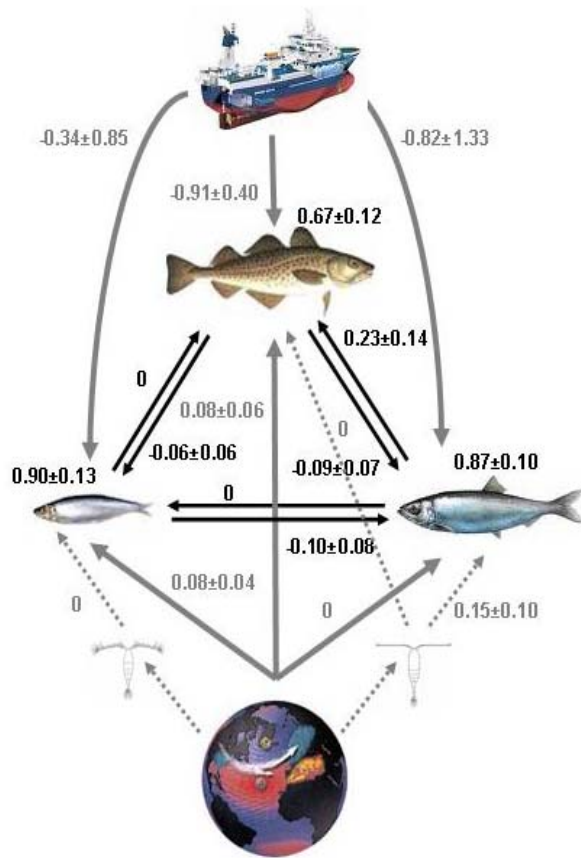


Fig. 4. A schematic view of the BALMAR model and the upper-trophic food-web of the Central Baltic Sea. Black arrows and parameters represent species interactions between cod (top), sprat (left) and herring (right). (Intra-specific parameters  $<1$  indicate an increasing degree of density dependence in the population). Grey arrows and parameters demonstrate the effects of fishing, climate and zooplankton on the three species respectively. (Interactions with the key zooplankton species *Acartia* spp. (left) and *Pseudocalanus acuspes* (right) are illustrated by dotted arrows). Zero parameter values indicate interactions excluded during model selection. (From Paper I).

Density dependence was detected for all species, with cod demonstrating a stronger degree of intraspecific competition compared to the prey species sprat and herring. This effect is likely related to juvenile predation (i.e., cannibalism) during periods of high cod SSB and a stronger degree of food competition and spatial overlap between age-classes (Neuenfeldt and Köster 2000). The density dependent effects on sprat and herring may primarily be explained by food competition (Möllmann et al., 2005) and egg cannibalism (Köster & Möllmann 2000). In addition, herring is negatively affected also by sprat competition (Möllmann et al., 2005), though the opposite is not supported by our analysis nor by

observations. Cod predation influence both prey species negatively (i.e., shown by the negative sign of the interaction parameters), while only herring demonstrate a significant net positive foraging effect on cod. Despite being an important prey item for cod, sprat predation on cod eggs may counteract this effect and as such underlie the lack of net positive foraging effect on cod (Köster & Möllmann 2000). As described in earlier sections, hydrographic change has markedly altered the Baltic Sea ecosystem through either direct or indirect pathways (Möllmann et al., 2008; Casini et al., 2009). In the final food-web model, a three year lagged positive effect of salinity on cod indicates a stronger direct effect on recruitment (i.e., through egg survival) than the availability of *Pseudocalanus acuspes*, the main food source for cod larvae (Köster et al., 2005). (The time-lag corresponds to the recruitment phase of Baltic cod reaching maturity at the age of four). Similarly, the positive effect of SST (i.e., lagged by one year) demonstrates a stronger direct effect on sprat recruitment (MacKenzie & Köster 2004), than the indirect response to increased prey availability of the warm-water copepod species *Acartia* spp. On the contrary, herring displays a stronger indirect climate effect as the availability *Pseudocalanus acuspes*, the key prey species for herring (Möllmann et al., 2005) proved a stronger predictor than direct variability in the physical environment. Concerning the effect of commercial fishing, we found a negative effect on all three species, with the largest effect on the heavily exploited cod population.

## 5.2 Recreating the variability of Central Baltic cod, herring and sprat

Based on the derived patterns of species interactions (i.e., the internal food-web dynamics) and the external forcing through fishing, zooplankton and climate (i.e., as described in the previous section 5.1) our fitted model clearly recreates the observed fish stock dynamics in the Baltic Sea from 1974-2004. These are characterized by a dramatic decrease of cod from high SSB levels during the early 1980s (Fig. 5a), an equally drastic increase in sprat SSB since the late 1980s (Fig. 5c), and a constant decline of herring SSB throughout the entire period (Fig. 5e). A way of validating the predictive capabilities of a model is to fit on a subset of the available data and then check the model by forecasting the remainder of the data (Chatfield 1989). Therefore, we adopted a sequential refitting procedure where the model was initially fitted to only the first ten years of the data set and then refitted and updated on a yearly basis, producing a prediction for each consecutive year. The predicted

values and associated 95% prediction intervals were compared with the observed values to assess the predictive accuracy of the model. Additionally, the food-web dynamics were simulated using only the first year values as initial conditions. This procedure is fundamentally different from a simple fit to the data, as the observed values from the second year onwards are not used (Hjermann et al., 2004). All simulations were run 1000 times with random process noise added at each time step. Mean values and a 95% confidence interval of the predictions were computed. Forced by the observed time-series of fishing mortalities and hydrographic variables (Fig. 5b, d, f), also the hindcasted simulations reproduce accurately the observed food-web dynamics during the period (see paper I).

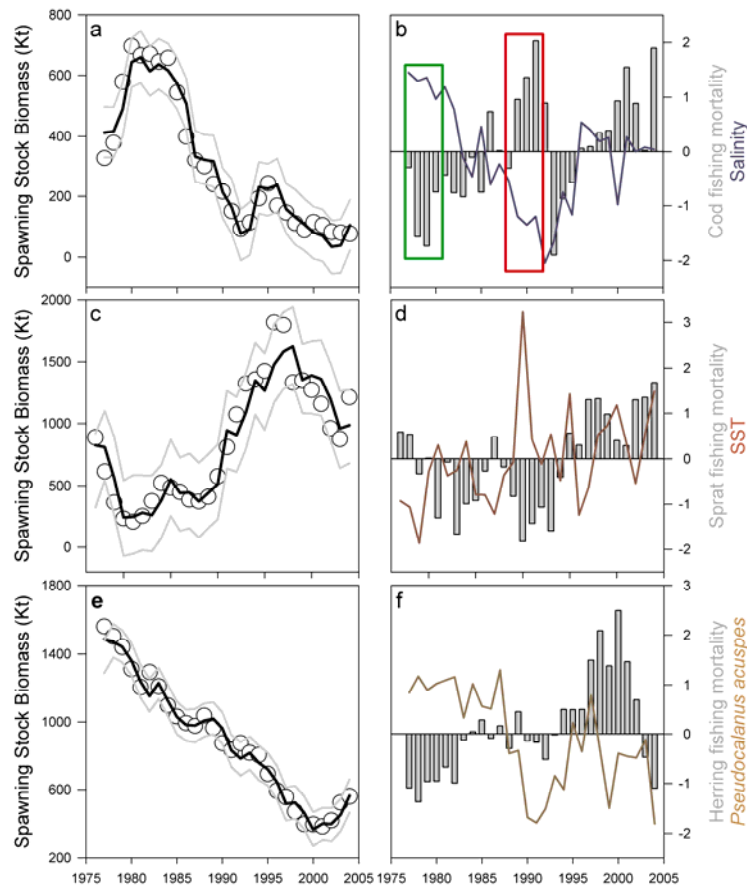


Fig. 5. Fitted (black) and observed biomasses (circles) of (a) cod, (c) sprat and (e) herring from 1977-2004. Prediction intervals are displayed by grey lines. The main external drivers are plotted as anomalies for each species respectively (b, d, f). In (b) a combination of low exploitation and record high salinities explain the sharp increase in cod during the late 1970s, i.e., the “gadoid outburst” (green box). On the contrary, decreasing salinities combined with high fishing pressure explain the dramatic decline and collapse of the cod stock in the early 1990s (red box). (From Paper I).

In the North Sea, the “gadoid outburst” (i.e., the strong and synchronous increase in several Atlantic cod stocks during the late 1970s) has been explained by indirect climate forcing due to “match-mismatch” in the timing and relative abundance of *Calanus finmarchicus* and *Calanus helgolandicus*, the key copepod prey species for growth and survival of North Sea cod larvae (Beaugrand et al., 2003). In our model, the “gadoid outburst” of Baltic cod is mainly explained by a period of historically low fishing mortalities in combination with record high salinities (Fig. 5b) following strong and frequent inflows of high saline and oxygenated water from the North Sea, thus enabling successful spawning and strong recruitment due to high egg and larvae survival in the entire Baltic Sea (Köster et al., 2005).

Though the ecological mechanisms differ between areas, the largely synchronous outburst of Atlantic cod stocks in the North and Baltic Seas suggests a common underlying driver. Since both variability in *C. finmarchicus* and *C. helgolandicus* as well as hydrographic conditions suitable for recruitment of Baltic cod (i.e., salinity and oxygen) has been strongly linked to oceanic inflow events from the North Atlantic (Matthaus & Franck 1992; Reid et al., 2003), climate driven changes in large-scale circulation patterns (Parsons & Lear 2001; Ottersen et al., 2001) seem the most likely driver.

Although variability in fishing pressure and changes in large-scale circulation patterns have contributed significantly to the observed dynamics of the prey species sprat and herring, the relative importance of internal species interactions seem stronger compared to the dynamics of their predator. Pronounced reductions in predation pressure following the collapse of the cod stock (Köster et al., 2003; Möllmann et al., 2008) in combination with temperature driven recruitment success (MacKenzie & Köster 2004) may therefore explain the drastic increase in sprat SSB observed (and simulated) during the period. The decrease in herring however, may primarily be explained by increased sprat competition, i.e., as the large sprat stock may presently more than compensate for the predatory release of cod, and decreasing availability of *Pseudocalanus acuspes* (Möllmann & Köster 2002; Voss et al., 2003). The effect of sprat competition is further evidenced by the decrease in size/age at maturation of herring observed during the period (Möllmann et al., 2005).

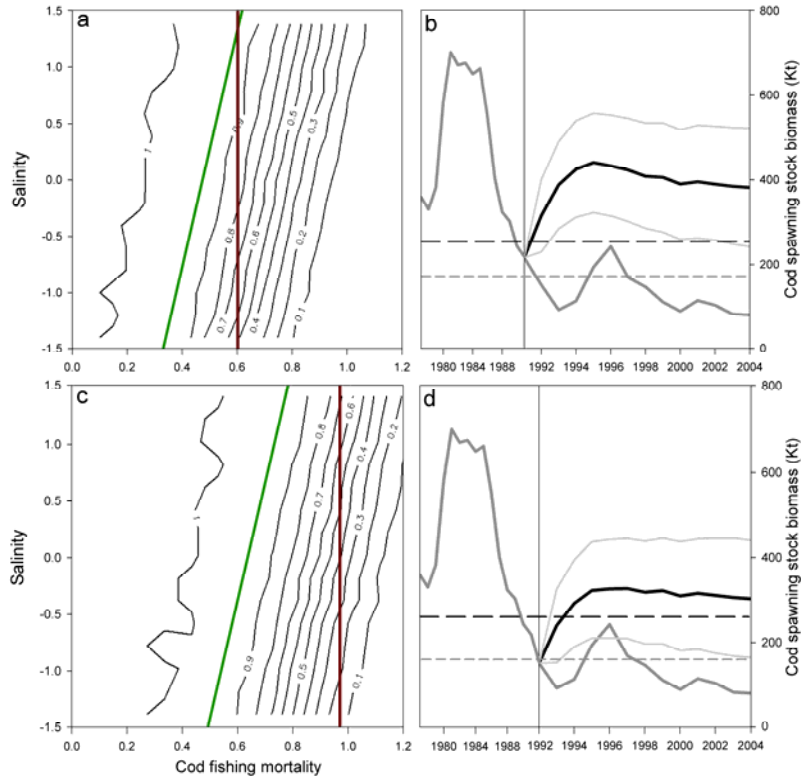


Fig. 6. The probability of cod stock recovery above  $B_{pa}$  (a) and  $B_{lim}$  (c) in 1992-2004 is shown over a range of exploitation and salinity levels (i.e., corresponding to observed salinity range from 1974-2004). The red vertical lines show the fixed reference levels,  $F_{pa}$  and  $F_{lim}$ , while the green diagonal lines show the adaptive management approach, deciding  $F$  levels based on salinity conditions. In (b, d) the dark-grey line represents the observed biomass and the black line the simulated biomass following the adaptive management strategy outlined in (a) and (c). Simulations are initialized in 1991 (b) and 1992 (d), the years following the collapse below  $B_{pa}$  and  $B_{lim}$  respectively. Light-grey lines indicate the upper and lower 95% confidence interval of the simulations. Horizontal lines define the ecologically safe levels  $B_{pa}$  (long-dash) and  $B_{lim}$  (short-dash). (From Paper I).

### 5.3 Adaptive management and cod stock forecasts under climate change

Based on the ability to hindcast the past food-web dynamics, we used the BALMAR model to explore whether given the present knowledge on climate effects, fishing and species interactions, we in hindsight could have managed the Baltic cod in ways such as to avoid the dramatic stock collapse in the early 1990s (Paper I). To that end, we formulated an adaptive management strategy accounting for both climate conditions and species interactions in setting precautionary exploitation levels (Garcia 1994). These exploitation levels were defined by first performing multiple stochastic simulations over a range of

fishing mortalities ( $F$  from 0-1.2) and salinity levels (i.e., corresponding to the observed salinity range from 1974-2004), where the response of the cod stock was calculated as the percentage of simulations where SSB recovers above the precautionary stock level ( $B_{pa}$ ) and the limiting stock level ( $B_{lim}$ ) in 1992-2004 respectively. Secondly, we assigned the precautionary exploitation levels relative to the observed salinity conditions during 1992-2004. As such, our adaptive management strategy increase exploitation during favourable salinity conditions, while during unfavourable conditions, lower exploitation levels compensate for recruitment reductions. In both scenarios, the probability of recovery above ecologically safe levels (i.e.,  $B_{pa}$  and  $B_{lim}$ ) increase with decreasing  $F$  and increasing salinity levels (Fig. 6a, c). When fished at  $F$  levels close to 0.3 and 0.5 the probability of recovery above  $B_{pa}$  and  $B_{lim}$  respectively approach 100% regardless of salinity conditions, while at exploitation above 1.0 and 1.2 a stock collapse seem inevitable. Our adaptive management simulations, initialized in 1991 and 1992 (i.e., the years following the collapse below  $B_{pa}$  and  $B_{lim}$ ), show that our precautionary management strategy, by adapting fishing pressure to climate conditions and species interactions, could significantly have prevented the cod stock from collapsing and promoted a recovery above ecologically safe levels (Fig. 6b, d).

Good decision making for fisheries and marine ecosystems requires a capacity to anticipate the consequences of management under different scenarios of climate change (Clarke et al., 2001). However, difficulties in evaluating impacts of climate change on marine ecosystems have resulted in a lack of reliable forecasts for fisheries production (Brander 2007). To study the effects of climate change on the dynamics of Baltic cod we developed a coupled climate–food web model approach (see section 4.5 and Fig. 3) in simulating four future scenarios for the Baltic Sea (Paper II). Due to large uncertainty in regionally downscaled climate scenarios for the Baltic Sea, i.e., dependent on the choice of GCMs outputs (Meier et al., 2006; BACC 2007), these scenarios aim to represent a number of probable “what if”-scenarios. The first “control scenario” without changes in climate conditions (i.e., salinity and SST) and at mean historical fishing levels, predicts an initial increase and future mean biomass fluctuating slightly above the limiting stock level ( $B_{lim}$ ) (Fig 7a). However, the lower 95% prediction interval is close to zero, indicating a small risk of extinction ( $< 2.5\%$ ) even without climate change. In the second scenario (Fig 7b), introducing a long-term change in SST ( $+3.5\text{ }^{\circ}\text{C}$ ) and salinity ( $-4.8\text{ psu}$ ) cause a probable extinction ( $>95\%$ ) of cod

by the mid-2060. The third scenario shows that if fishing is reduced according to previously recommended reference levels ( $F_{pa}$ ) then extinction may be postponed another 20 years (Fig 7c), by which time the salinity drops below the absolute threshold level for cod recruitment in the Baltic Sea (Köster et al., 2005). In the final scenario, a minor decrease in salinity by 0.8 psu (i.e., the most conservative prediction for salinity levels in 2071-2100), may still not promote long-term persistence of the cod stock if exploitation is kept at  $F_{pa}$  (Fig. 7d). Hence, a strategy for adapting fishing mortalities to climate driven stock production is necessary to ensure the existence of Baltic cod in the 22<sup>nd</sup> century.

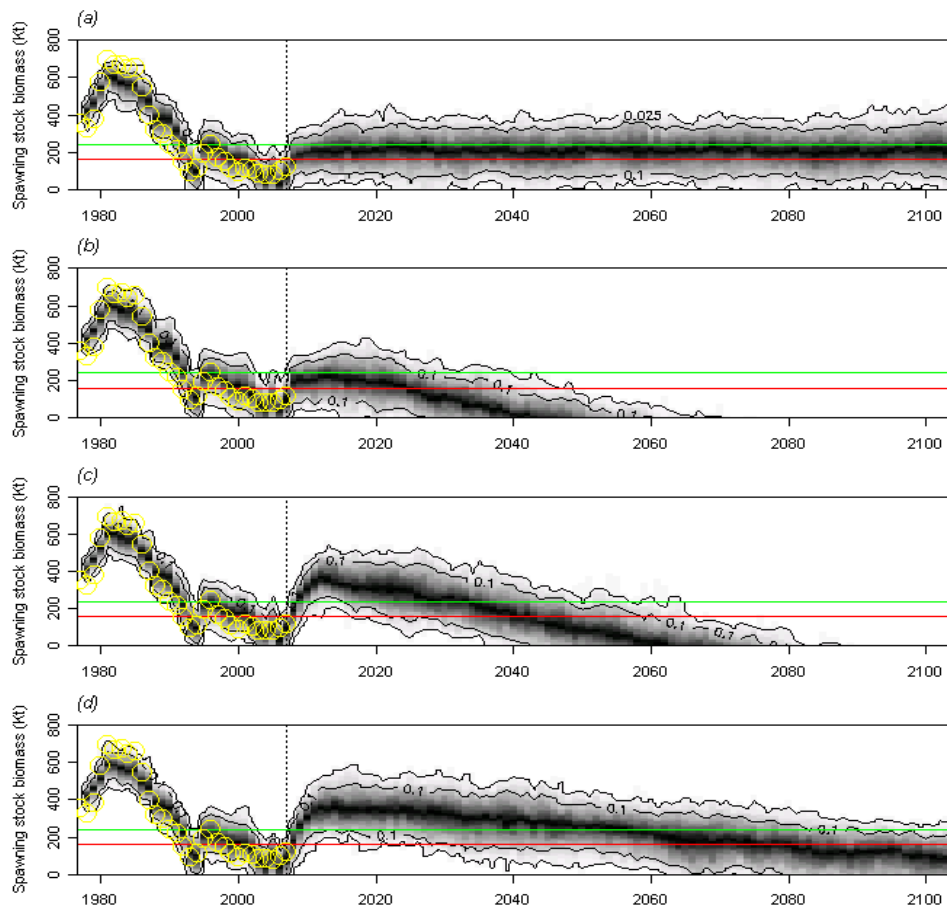


Fig. 7. Forecasts of cod SSB under different climate and management scenarios. In (a) salinity, SST and  $F$  remain at mean 1974-2004 levels. Hindcasted simulations are compared with observed SSB (yellow circles) as to validate the predictive accuracy of the model. (b) Increase in SST by  $3.5^{\circ}\text{C}$  and decrease in salinity by 4.8 psu combined with mean  $F$  levels. (c) As in (b) but with  $F$  reduced to  $F_{pa}$ . (d) Fishing at  $F_{pa}$  but with a predicted decrease in salinity by only 0.8 psu. Horizontal lines show the precautionary stock level,  $B_{pa}$  (green) and limiting stock level,  $B_{lim}$  (red). Black contour lines indicate prediction intervals within which the cod stock dynamics of each replicated run fluctuates. (From Paper II).

In order to demonstrate that our adaptive management strategy is essential in preventing future stock collapses we simulated a set of long-term dynamics of Baltic cod under three different management scenarios: (i) fishing mortalities fluctuate at mean historical levels (1974-2004); (ii) fishing mortalities remain fixed at  $F_{pa}=0.6$ ; (iii) fishing levels are adapted to salinity conditions (i.e.,  $F$  varies according to  $0.6 \pm 0.3$ ). Forced under the same climate conditions only the adaptive management approach may prevent future stock collapses and maintain the stock stably above ecologically sustainable levels (Fig. 8c). Though the fixed reference approach may reduce large-scale variability in SSB (Fig. 8b) compared to a more “random” harvesting scenario (Fig. 8a) it does not sufficiently buffer against climate driven recruitment failure nor prevent recurrent stock collapses (paper I).

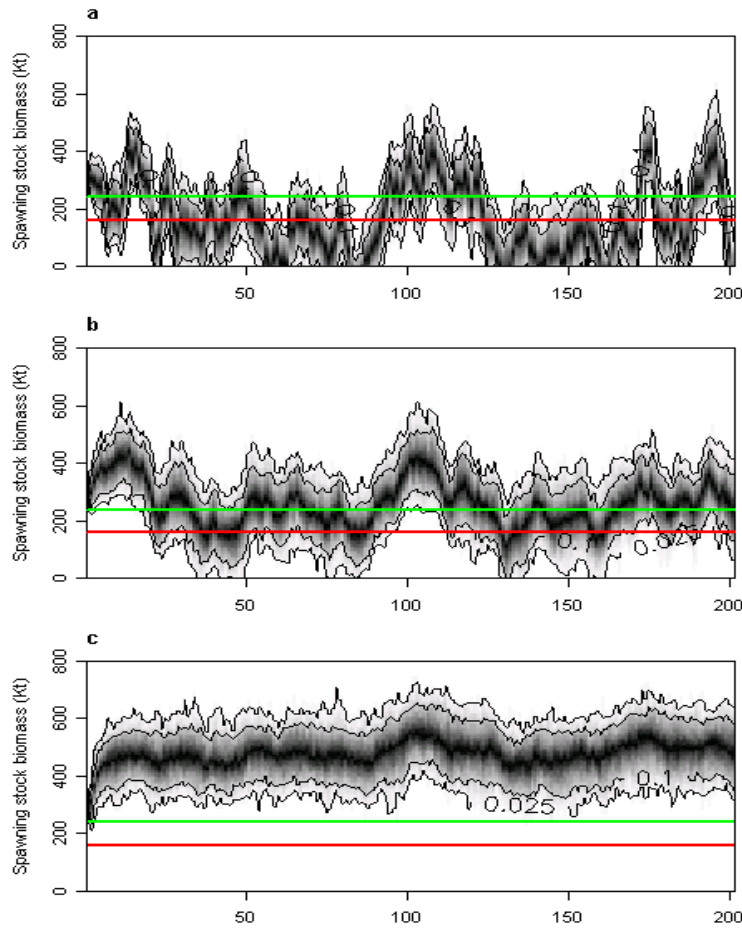
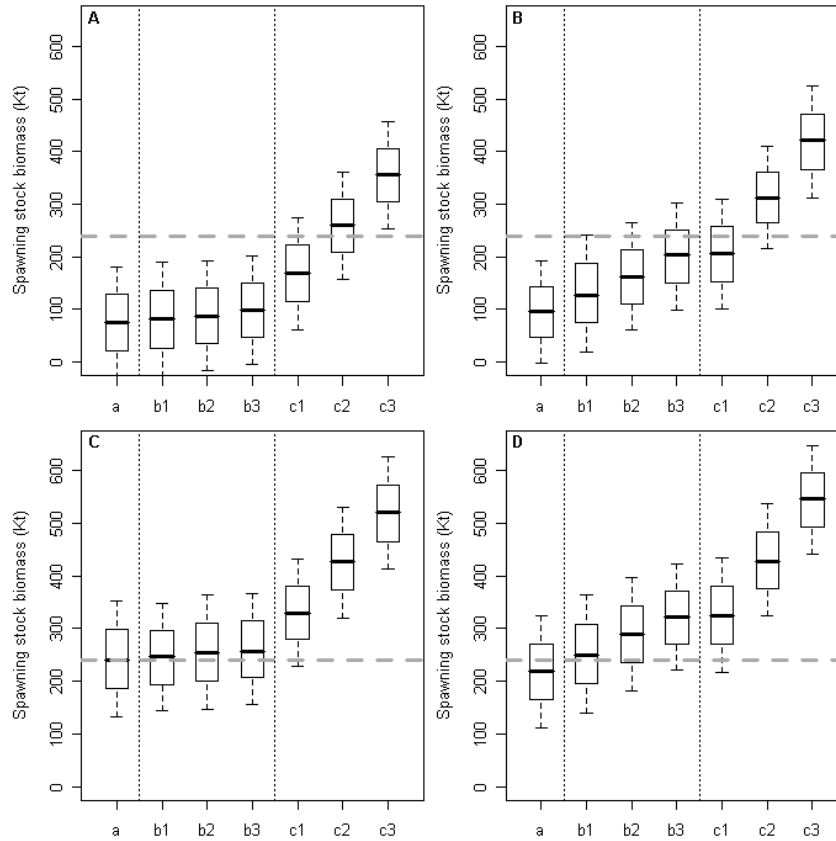


Fig. 8. Simulated dynamics of Baltic cod under different management scenarios: (a) fishing mortalities fluctuate at mean historical levels; (b) fishing mortalities are fixed at  $F_{pa}$  (0.6); (c) fishing levels are adapted to salinity conditions (i.e.,  $F = 0.6 \pm 0.3$ ). Solid horizontal lines mark the recommended ecologically safe levels of Baltic cod, the precautionary stock level,  $B_{pa}$  (green) and limiting stock level,  $B_{lim}$  (red). Black contour lines show the 90% and 95% prediction intervals within which the cod stock dynamics of each replicated run fluctuates. (From Paper I).



#### 5.4 Food-web interactions and multi-species management in the Baltic Sea

In order to promote a recovery of the Baltic cod, large-scale biomanipulation has been suggested a possible management approach (Carlgren 2007). By selective fishing on sprat, this approach aims to weaken the negative feedbacks on cod recruitment, i.e., egg predation (Köster & Möllmann 2000), and reinstate top-predator regulation in the open and coastal areas of the Baltic Sea. Using the BALMAR model we simulated a number of management scenarios including large-scale biomanipulation of sprat (i.e., a reduction in SSB by >75% over three consecutive years) and evaluated their ecological, operational and economic effects on promoting a recovery of Baltic cod (paper III).



**Fig. 9.** Simulated SSB of Baltic cod under management scenarios (a-c), where scenario (a) refers to mean F levels, scenarios (b1-b3) to a 25, 50 and 75% reduction in sprat SSB and scenarios (c1-3) to a 25, 50 and 75% reduction in cod F. The short- (left) and long-term response (right) of the cod stock are shown for two climate regimes, resembling alternating periods of unfavorable (A, B) and favorable (C, D) hydrographic conditions for cod recruitment. The dashed line represents the precautionary stock size ( $B_{pa}$ ) above which the cod stock is considered as recovered to ecologically safe levels. Upper and lower confidence intervals are shown for each scenario. (From paper III).

Our model simulations show that biomanipulation would be largely ineffective in restoring the cod stock, while reductions in cod  $F$  or increasing salinity levels would cause a rapid increase above ecologically safe levels (Fig. 9). We argue that this is due to the lower importance of the two suggested feedback mechanisms, i.e., egg and *P. acuspes* predation relative to the direct effects of hydrography (i.e., salinity and oxygen conditions) on cod recruitment. The reason behind this limited effect may be that also the feedback mechanisms are critically dependent on the hydrographic situation and hence are reflected in the strong effect of salinity on cod in our model. During low salinity conditions cod eggs float deeper in the water column increasing the spatial overlap with sprat thus adding to the direct mortality caused by low salinity via low oxygen conditions (Köster & Möllmann 2000).

### *5.5 Bio-economic considerations and optimal management*

Being able to account for management consequences over a range of policy objectives, including both ecological and economic aspects is of vital importance in implementing a successful EBFM approach (Hilborn 2007). To that end, we coupled the BALMAR food-web model to a simple bio-economic model (see section 4.6) aiming to compare net revenues of the Baltic cod fishery under a fixed- and adaptive management strategy respectively (Paper I). NPVs were calculated over a range of exploitation levels ( $F$  from 0-1.2) and fishermen discount rates (0-15%) by simulating the yield- and stock dynamics of Baltic cod over a 20-year period. Simulations were initiated at mean SSB levels for all species and run with salinity and SST conditions fluctuating at mean historical levels.

In all simulations, the adaptive management strategy (Fig. 10b) yields net revenues considerably higher than the fixed management strategy (Fig. 10a). Hence, we argue that our adaptive management strategy would not only be ecologically but economically profitable due to increased landings and reduced fishing costs as the stock and hence the catchability is allowed to increase. These results support the recent findings of the importance and gain of investing in “natural capital” (i.e., in future stock size) as a long-term management strategy for Baltic cod (Döring & Egelkraut 2008).

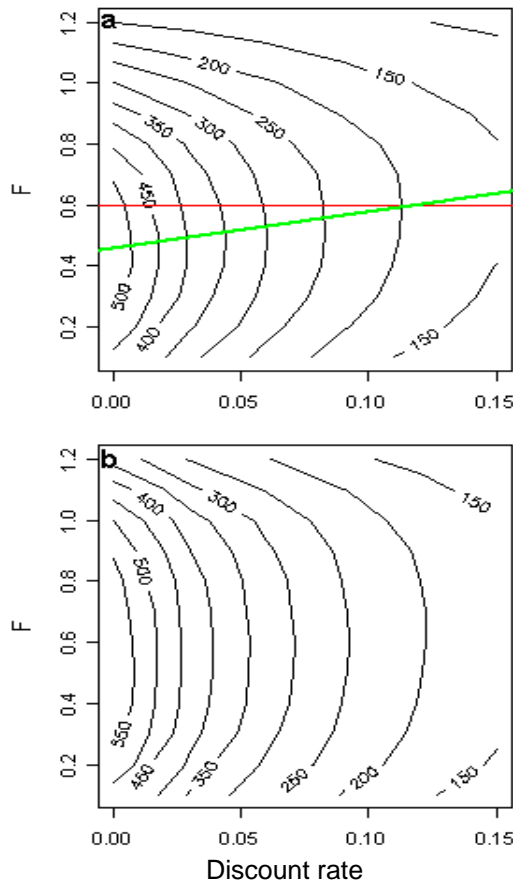
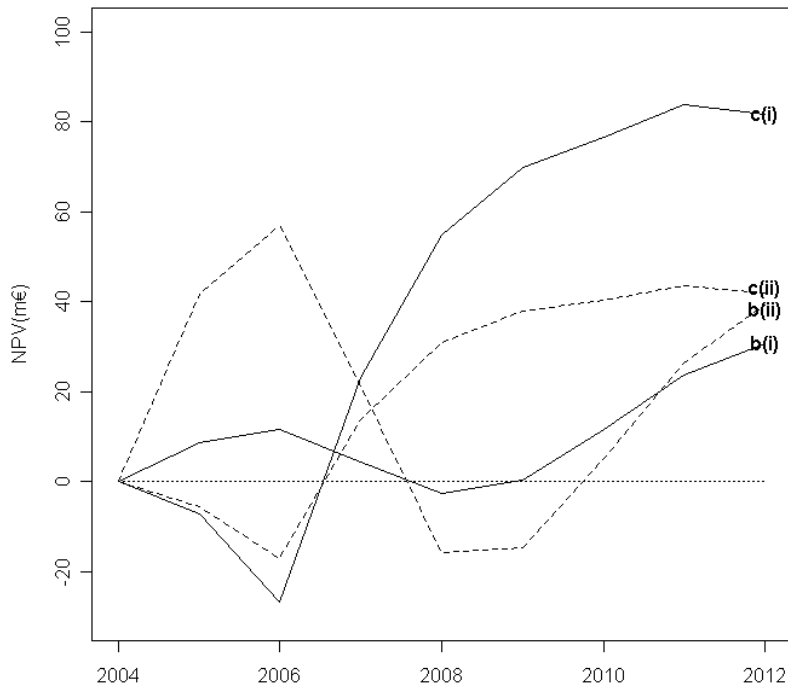


Fig. 10. Revenue of the Baltic cod fishery under a (a) fixed- and (b) adaptive management strategy. Net Present Values (NPVs) are shown over a range of fisherman discount rates (0-15%) and fishing mortalities ( $F$  from 0-1.2). The economically optimal exploitation levels ( $F_{opt}$ ) is shown in green, while the horizontal red line marks the precautionary fishing mortality,  $F_{pa}$ . (From paper I).

In another study, we used the coupled ecological-bio-economic model approach to perform a brief analysis comparing the economic consequences of sprat biomanipulation (i.e., scenario b) and reductions in cod  $F$  (i.e., scenario c) respectively (paper III). Since no reliable estimates of fishing cost are available for sprat and herring, we calculated the NPVs of future landings without subtracting fishing costs in both management scenarios.

Following the drastic reductions in sprat SSB, the rapid increase in sprat landings cause short-term revenues of scenario (b) to increase, only to be followed by a drastic decrease in NPVs as the sprat stock approaches a minimum stock size in 2008 (Fig. 11). Corresponding to the gradual increase in cod SSB, NPVs then rise gradually above reference levels. In management scenario (c), NPVs show an initial decrease due to declining cod landings (Fig. 11). However, as the cod stock recovers, landings increase with a net annual revenue reaching 40-80 m€. Since the simulated average gross primary value per year (i.e., the average value of landings per year) corresponds closely to observed levels (STECF 2004, 2005), our simulations may represent likely estimates of the total economic value of the Baltic Sea fishery under different management scenarios.

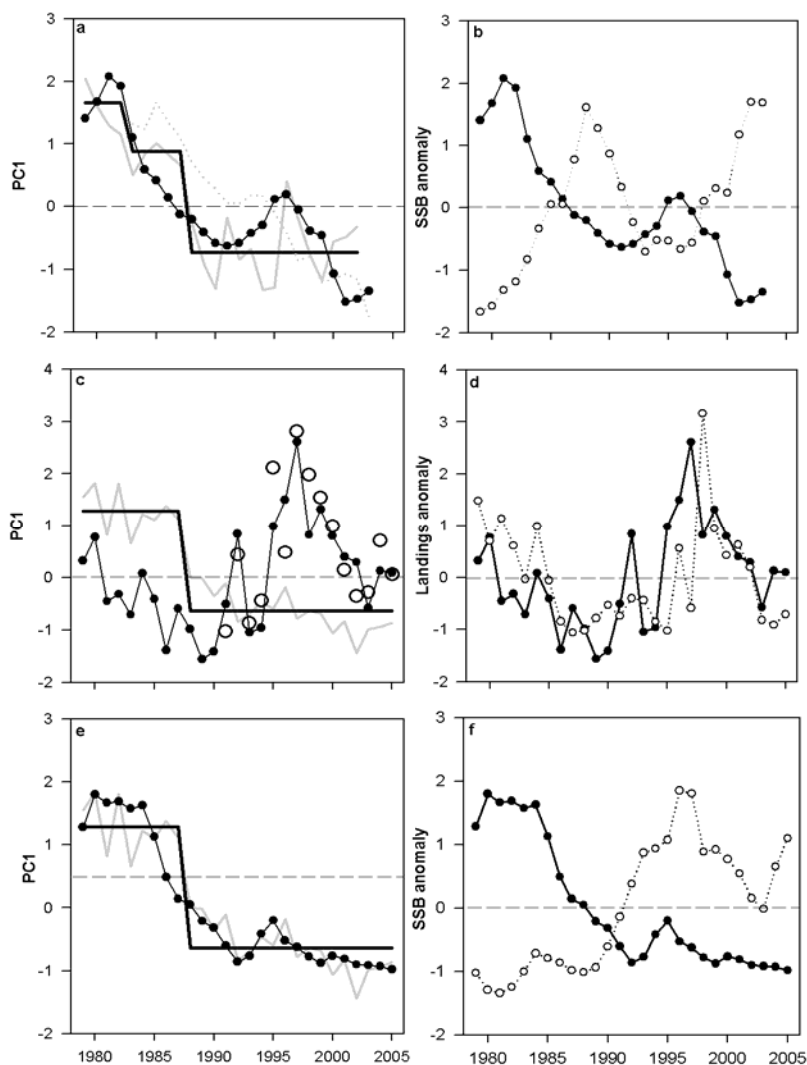


**Fig. 11.** Annual NPVs for scenario (b) and (c) from 2004-2012. The NPVs are calculated as the net economic value (m€) of the scenario with reference to the status-quo, “control” scenario (a), shown as a dotted line. b(i) and c(i) refer to the NPVs based on a fixed market price of cod, sprat and herring while b(ii) and c(ii) show NPVs calculated on market price as a function of supply, i.e., landings. (From paper III).

### 5.6 Overfishing and the Resilience of Marine Ecosystems

By reducing the age, size, and geographic diversity of populations, overfishing has been shown to increase the sensitivity of fish stocks to recruitment stress (Brander 2005; Ottersen et al., 2006; Anderson et al., 2008), thus degrading their resilience to withstand and buffer against climate change (Folke et al., 2004). In a cross-ecosystem comparison between the North Sea, Central Baltic Sea and the Sound (paper IV), the areas show similar ecosystem dynamics and timing of regime shifts (Fig. 12), i.e., as illustrated by PC1 scores from ecosystem assessments in these areas (Weijermann et al., 2005; Möllmann et al., 2009, paper IV). On the contrary, while the dynamics of North Sea and Baltic Sea cod stocks follow the ecosystem dynamics (Fig. 12a, e), the Sound cod stock shows an increase since the mid-1990s (Fig. 12c). The recovery potential of the Sound cod stock is likely due to the absence of trawl fishing (Svedäng et al., 2004), yielding demographic conditions in terms of age- and size-distribution far better than the overexploited neighbouring stocks (Svedäng et al., 2002). With many large, old and experienced individuals and several generations contributing to spawning (Ottersen et al., 2006; Anderson et al., 2008), the Sound cod stock seem more resilient to recruitment stress and could therefore recover following years of potentially unfavourable climate conditions for spawning.

Furthermore, marine ecosystems are considered bottom-up driven, while top-down forcing is thought to represent a form of biological instability (Strong 1992). In the North and Baltic Seas, the regime shift and collapse of the cod stocks triggered a trophic cascade causing changes in the lower trophic levels (Casini et al., 2008; Kirby et al., 2009). The trophic cascade is illustrated by the strong negative correlation between cod and sprat ( $r = -0.72$ ,  $p < 0.001$ ), the dominating planktivorous species in the Baltic Sea (Fig. 12f) and between cod and herring ( $r = -0.81$ ,  $p < 0.001$ ), one of the main planktivorous fish species in the North Sea (Fig. 12b). As opposed to the neighbouring areas, the positive relationship between the Sound cod and herring ( $r = 0.63$ ,  $p < 0.001$ ) indicates no trophic cascade, instead a strong bottom-up regulation. Our findings support the need for maintenance and restoration of ecosystem resilience in marine ecosystem management and conservation (Folke et al., 2004).



**Fig. 12.** Comparison of PC1 scores (grey), SSB of cod (solid) and pelagic fish species (dotted) from the North Sea (a, b), the Sound (c, d) and the Central Baltic Sea (e, f). Herring is shown for the North Sea and the Sound, while sprat is shown for the Central Baltic Sea. (Additionally, PC1 scores (dotted) from Kenny et al. (2009) are shown for the North Sea). Solid black lines represent the regime shifts as detected by the STARS method. Cod landings from the Sound are compared with normalized survey data available from 1991-2006 (circles). (From paper IV).

## **6. Conclusions and future perspectives**

In a recent review in *Science* concerning the status of marine fisheries, Europe (and the Baltic Sea in particular) stand out as a striking example of irresponsible management, demonstrating highly overexploited fish stocks overall (Worm et al., 2009). In order to overcome the structural failures of fisheries management within Europe, a “toolbox with which to meet our policy objectives and targets, taking account of regional specificities” is essentially needed (Speech by Commissioner Borg, Brussels, 29<sup>th</sup> June 2009). Since policy decisions must be based on robust and sound knowledge on the level of exploitation that stocks can sustain, of the effects of fishing on marine ecosystems and on the impacts of climate change, improving the scientific knowledge is of vital importance in the upcoming revision of the Common Fisheries Policy (CFP) of the European Union, the so-called “Green paper” (EC 2009).

This Ph.D. project aims to provide a first step towards reversing this situation and put European fisheries in the forefront of sustainable marine development worldwide. As such, this Ph.D. project may not only contribute to the scientific state-of-the-art in integrated marine ecosystem modelling, by (i) furthering our understanding of the relative roles and synergies between different external and internal ecosystem drivers, (ii) increasing ecological realism in fisheries assessment models, and (iii) providing cross-disciplinary exchange of scientific concepts and ideas with climatologists, oceanographers and bio-economists, but through its communication with stakeholders and managers nationally and internationally (i.e., within ICES) fill an important knowledge gap and stimulate the development and implementation of ecosystem-based marine and fisheries management within EU and beyond.

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In all aspects of this Ph.D. project, from scientific content to administrative arrangements, I have strived to embrace the concept of holistic integration and cross-disciplinary confusion at multiple temporal and spatial scales. To that end, as a Swedish Ph.D. student matriculated at the University of Copenhagen (Denmark), I embarked on the (European) Marie Curie EST project METAOCEANS, co-ordinated from San Sebastian (Spain), set up office at the National Institute of Aquatic Resources (Denmark) under supervision from the University of Hamburg (Germany). To complicate things even further, I collaborated with the Centre for Ecological and Evolutionary Synthesis (CEES) at the University of Oslo (Norway) and the department of Theoretical Ecology at Lund University (Sweden) along the way. Before continuing, allow me to more properly introduce the key characters in this intriguingly complicated plot of researchers and institutes to whom I wish to send my warmest and sincerest thanks while completing this Ph.D.

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Martin Lindegren



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# Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach

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Worldwide a number of fish stocks have collapsed because of overfishing and climate-induced ecosystem changes. Developing ecosystem-based fisheries management (EBFM) to prevent these catastrophic events in the future requires ecological models incorporating both internal food-web dynamics and external drivers such as fishing and climate. Using a stochastic food-web model for a large marine ecosystem (i.e., the Baltic Sea) hosting a commercially important cod stock, we were able to reconstruct the history of the stock. Moreover we demonstrate that in hindsight the collapse could only have been avoidable by adapting fishing pressure to environmental conditions and food-web interactions. The modeling approach presented here represents a significant advance for EBFM, the application of which is important for sustainable resource management in the future.

ecosystem-based fisheries management | sustainability

Atlantic cod (*Gadus morhua*) is among the commercially most important fish species of the European waters. Many of the stocks have declined dramatically and still remain at historically low levels (1, 2). These collapses have largely resulted from overfishing (3, 4) and climate-driven declines in productivity (5, 6). The climate effect generally works through changes in the physical environment (e.g., temperature and salinity), but also through altered food supply for early life-history stages, eventually affecting recruitment (5, 6). In accordance with this effect, recruitment failure of Eastern Baltic cod was caused mainly by high egg and larval mortalities as a result of climate-induced hydrographic change (7, 8). In several areas the collapses of cod stocks were part or major drivers of large-scale reorganizations of ecosystems (9). These so-called regime shifts are frequently caused by climatic changes (9, 10) and/or over-exploitation resulting in cascading trophic interactions (11, 12). Similarly to other areas, the Baltic Sea underwent both regime shifts and trophic cascades (8, 13). Such alterations in ecosystem structure typically affect species interactions, eventually influencing food-web dynamics through both positive and negative feedback loops (14).

The recognition of the ecosystem context in the collapse of fish stocks has led to the development of more holistic ecosystem-based fisheries management (EBFM) approaches (15, 16). To be of value in decision making and management, ecosystem-based models require a manageable degree of complexity, to incorporate ecological detail, represent environmental and fishing effects, and provide estimates of uncertainty (17, 18). Statistical models have proven useful in incorporating key ecological and environmental drivers and evaluating multiple sources of uncertainty (19–21), an advantage over existing multispecies models for the Baltic Sea (22, 23). Multivariate autoregressive models [MAR(1)] provide a statistical framework for modeling food-web interactions at multiple trophic levels (14). Within this modeling framework, stochastic events such as environmental variability can be included to account for external forcing on the system's dynamics. By integrating multiple drivers and uncertainties the MAR(1) framework thus provides an important tool

for EBFM. Surprisingly, it has rarely been extended beyond theory, and its application to real food webs (24, 25) has, to our knowledge, never been used in fisheries management.

We applied the MAR(1) approach to the food web of the Baltic Sea, host to one of the formerly most productive cod stocks (7). The Baltic Sea upper trophic food web is dominated by cod and two competing planktivorous fish species, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Additionally, the species are forced top-down by fishing and bottom-up through zooplankton and environmental effects (Fig. 1). We modeled this simple food web by fitting a MAR(1) state-space model to a time series of population biomasses, fishing mortalities ( $F$ ), and a number of abiotic and biotic variables, selected based on prior knowledge of their effects on fish stocks (see Table S1 and SI Text). Finally, the most parsimonious model in terms of the number of parameters and the explained variance was selected (Table S2 and Fig. S1).

## Model Results and Validation

Model parameters of the selected model (Tables S3–S6) accurately captured the known mechanisms of species interactions within the food web and the effects of fishing, zooplankton, and environmental variability on the three species (Fig. 1). Density dependence was detected for all species. The strong effect on cod probably is caused by cannibalism (26), whereas food competition (27) and egg cannibalism may explain the effect on herring and sprat (28). Herring is additionally affected by sprat competition (27), although the opposite is not seen. Cod predation influences both prey species negatively, whereas only herring shows a significant net positive foraging effect on cod. Sprat predation on cod eggs may underlie the lack of positive effect on cod (29).

Climate-induced hydrographic change has markedly altered the Baltic Sea ecosystem (8, 13). Changes in salinity and oxygen conditions act both directly on cod recruitment (i.e., through egg and larval survival) or indirectly on the availability of *Pseudocalanus acuspes*, the main food source for larval cod (7). In our model, a 3-year lagged positive effect of salinity indicates a stronger direct environmental effect (Fig. 2B). The time lag corresponds to the recruitment phase of Baltic cod reaching maturity at the age of 4. Sea surface temperature (SST) lagged by 1 year strongly affects sprat (Fig. 2D), demonstrating its positive effect on recruitment (30). Although increased prey availability may indirectly add to this effect (30), the interaction with *Acartia* spp. did not significantly explain the variance in sprat spawning stock biomass (SSB). On the contrary, our model

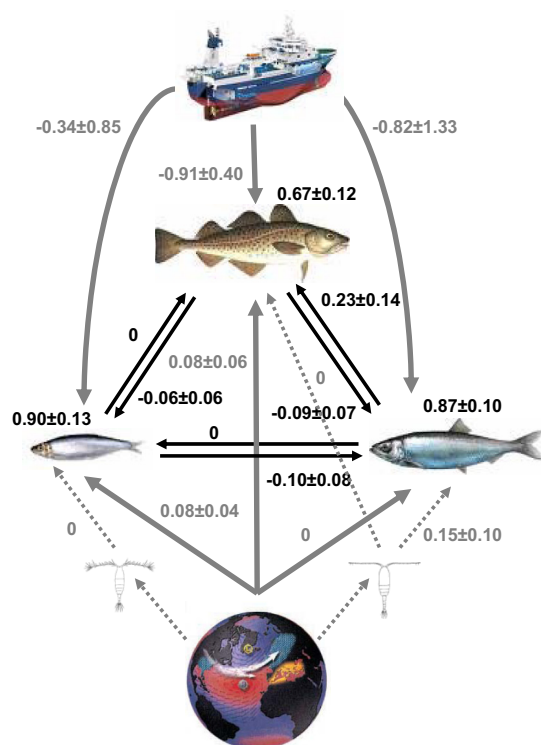
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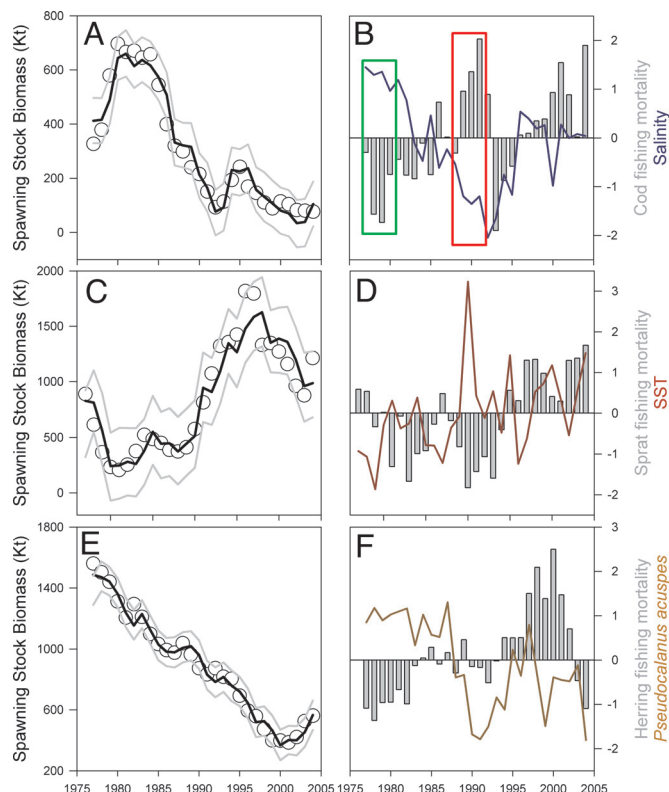


**Fig. 1.** A schematic view of the Baltic Sea upper-trophic food web. Black arrows and parameters represent species interactions between cod (Top), sprat (Left), and herring (Right). Gray arrows and parameters demonstrate the effects of fishing, climate, and zooplankton on the three species. Interactions with the key zooplankton species *Acartia* spp. (Left) and *P. acuspes* (Right) are illustrated by dotted arrows. Negative parameter values indicate negative effects on the biomass of the species and vice versa. Intraspecific parameters  $<1$  indicate an increasing degree of density dependence in the population. Zero parameter values indicate interactions excluded during model selection. Note that even though it is statistically uncertain we decided to include the fishing effect on sprat and herring because they are heavily exploited by commercial fishing. Climate image is from [www.ideo.columbia.edu/res/pi/NAO](http://www.ideo.columbia.edu/res/pi/NAO).

displays a significant effect of *P. acuspes* on herring (Fig. 2F). With *P. acuspes* being a key prey species for herring (27), this interaction indicates a stronger indirect environmental effect on herring, i.e., because *P. acuspes* critically depends on high salinities for reproduction (31). We found a negative effect of commercial fishing on all three species, with the largest effect on cod.

By combining internal food-web dynamics with external forcing through fishing, zooplankton and the physical environment our fitted model clearly reproduces the observed fish stock dynamics in the Baltic Sea. These are characterized by the decrease of cod from high levels during the early 1980s (Fig. 2A), the drastic increase of sprat since the late 1980s (Fig. 2C), and a constant decline of herring (Fig. 2E). We validated our model by sequentially refitting the model for varying time periods and hindcasting the observed dynamics based on only the starting biomass values (Fig. S2). Forced by the observed time series of fishing mortality and salinity (Fig. 2B) the simulations recreate accurately both the sharp increase in cod biomass of the late 1970s, the so-called “gadoid outburst,” and the dramatic decline and collapse of the stock in the early 1990s (Fig. S2b).

The gadoid outburst in the North Sea has been explained mainly by indirect climate forcing caused by “match–mismatch” in the timing and abundance of key copepod prey for larval cod (i.e., *Calanus finmarchicus* and *Calanus helgolandicus*; ref. 5). In our model, the gadoid outburst of Baltic cod is explained mainly

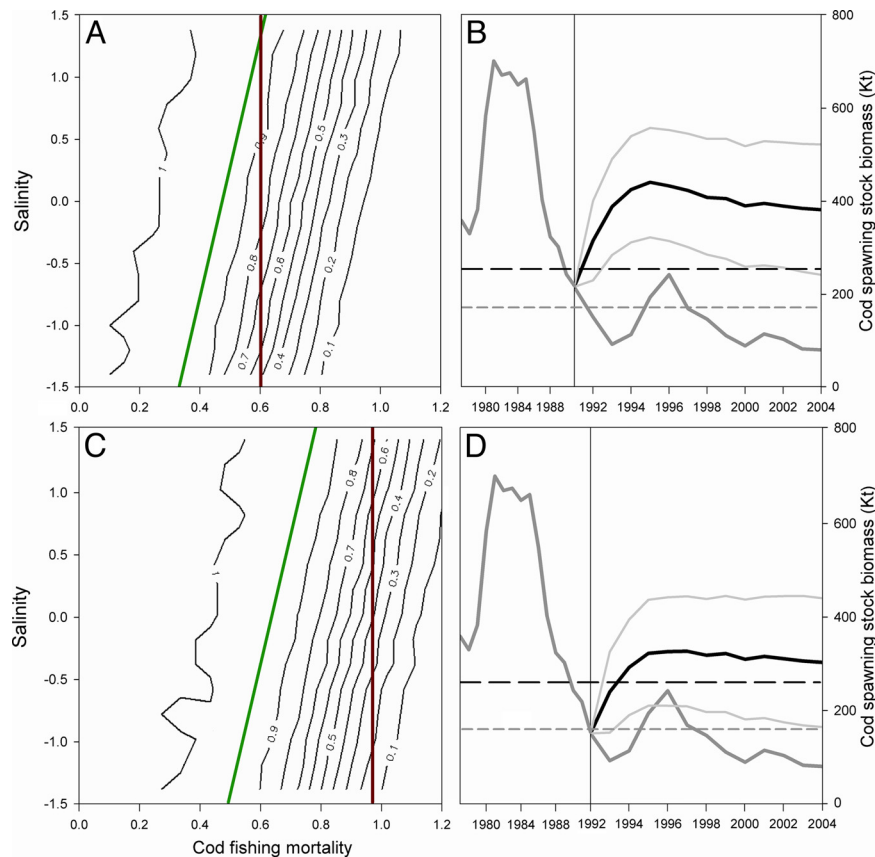


**Fig. 2.** Historical development of the Baltic Sea fish populations. (A, C, and E) The fitted biomass values (black lines) represent well the observed biomasses (circles) of cod ( $r^2 = 0.95$ ) (A), sprat ( $r^2 = 0.89$ ) (C), and herring ( $r^2 = 0.98$ ) (E) from 1977 to 2004. Upper and lower 95% prediction intervals are displayed by gray lines. (B, D, and F) The main external drivers, i.e., fishing mortalities and environmental variables are shown as anomalies (i.e., standardized to zero mean and unit variance) for each species. In B a combination of low fishing mortalities and record high salinities explains the sharp increase in cod during the late 1970s, i.e., the gadoid outburst (green box). On the contrary, decreasing salinities combined with high fishing pressure explain the dramatic decline and collapse of the cod stock in the early 1990s (red box).

by a period of anomalously low fishing mortalities in combination with record high salinities (Fig. 2B), enabling successful spawning and strong recruitment caused by high egg and larvae survival in the entire Baltic Sea (7, 32). Although the ecological mechanisms differ between areas, the largely synchronous outburst of cod in the North and Baltic Seas suggests a common underlying driver. Because both variability in *C. finmarchicus* and *C. helgolandicus* and hydrographic conditions suitable for recruitment of Baltic cod (i.e., salinity and oxygen) have been strongly linked to oceanic inflow events from the North Atlantic (33, 34), climate-driven changes in large-scale circulation patterns (35, 36) seem to be the most likely driver.

### Management Scenarios and Simulations

The validated model was then used to explore whether given the present knowledge on environmental forcing and species interactions, we in hindsight could have managed the cod stock in ways to avoid a collapse. To this end we applied an adaptive management approach (37), taking into account both environmental conditions and food-web interactions in deciding precautionary exploitation levels for Baltic cod. First, to derive precautionary exploitation levels (38), we performed multiple stochastic simulations over a range of fishing mortalities ( $F$  from 0 to 1.2) and salinity levels (i.e., corresponding to the observed salinity range from 1974 to 2004). The response of the cod stock was calculated as the percentage of simulations where SSB



**Fig. 3.** An adaptive management strategy for Baltic cod. (A and C) The probability of cod stock recovery above  $B_{pa}$  (A) and  $B_{lim}$  (C) in 1992–2004 is shown over a range of fishing mortalities ( $F$  from 0 to 1.2) and salinity levels (i.e., corresponding to the observed standardized salinity range from 1974 to 2004). The red vertical lines show the recommended fixed reference levels,  $F_{pa}$  and  $F_{lim}$ , and the green diagonal lines show the adaptive management approach deciding  $F$  levels based on salinity conditions. (B and D) The dark gray line represents the observed biomass and the black line represents the simulated biomass following the adaptive management strategy outlined in A and C. The simulations are initialized in 1991 (B) and 1992 (D), the years after the collapse below  $B_{pa}$  and  $B_{lim}$ , respectively. Light-gray lines indicate the upper and lower 95% confidence interval of the simulations. Horizontal lines define the ecologically safe levels  $B_{pa}$  (long dash) and  $B_{lim}$  (short dash) above which the stock is considered recovered.

recovers above the precautionary stock level ( $B_{pa}$ ) and the limiting stock level ( $B_{lim}$ ) in 1992 and 2004, respectively, providing a measure of the probability of stock recovery above ecologically safe levels.

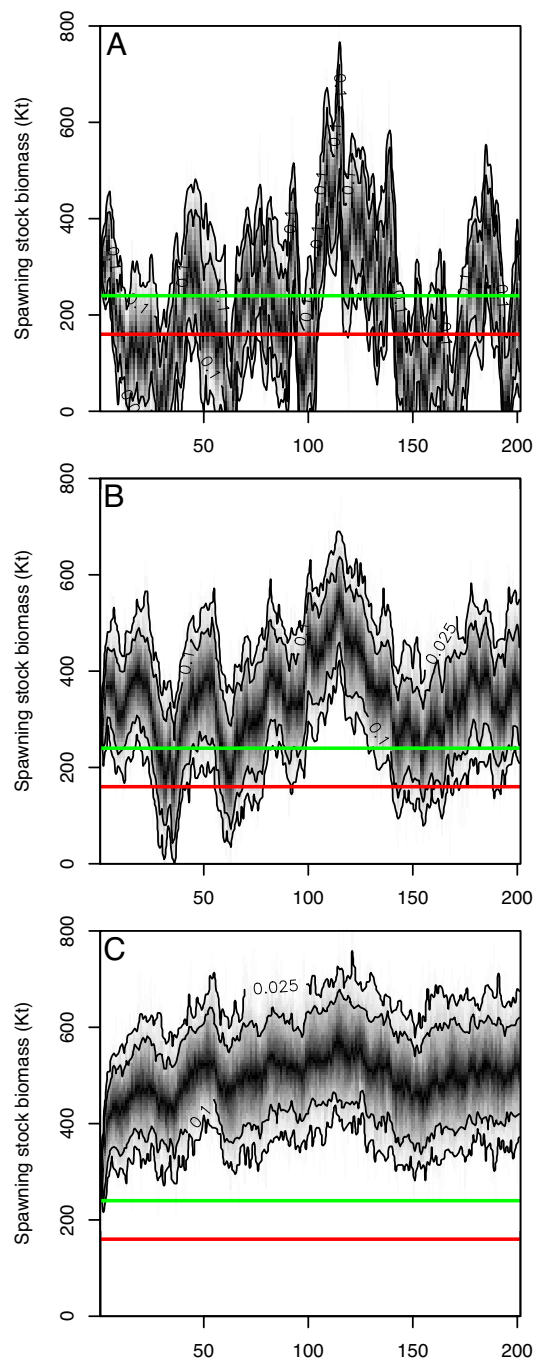
In both scenarios the probability of recovery increase rapidly with decreasing  $F$  and increasing salinity levels (Fig. 3 A and C). At  $F$  levels close to 0.3 and 0.5 the probability of recovery above  $B_{pa}$  and  $B_{lim}$ , respectively, approach 100% regardless of salinity level, whereas at exploitation  $>1.0$  and 1.2 a collapse below ecologically safe levels is inevitable. It is noteworthy that the actual  $F$  before the collapse and in several recent years were well above this critical threshold (e.g., 1.41 in 1991 and 1.29 in 2004). During a period of highly unfavorable salinity conditions for spawning and recruitment (i.e., because of a lack of inflows from the North Sea) these extreme exploitation levels (Fig. 2B) no doubt caused the decline and collapse of Baltic cod (7). Furthermore, when fished according to the previously recommended reference levels, the precautionary fishing mortality ( $F_{pa}$ ) may promote a stock recovery above  $B_{pa}$  only during highly favorable salinity conditions, whereas at the limiting fishing mortality ( $F_{lim}$ ) not even maximum observed salinity levels can guarantee a recovery above  $B_{lim}$ . Hence, fixed reference levels not taking into consideration environmental forcing and indirect effects of food-web interactions seem far from precautionary and would not have promoted a recovery of the stock.

Based on the above analysis of recovery potential at different environmental conditions we formulated our adaptive

management strategy by assigning exploitation levels relative to the observed salinity conditions during 1992–2004. As such, our adaptive strategy allow  $F$  levels to increase during favorable salinity conditions, whereas during unfavorable conditions lower  $F$  levels may compensate for recruitment reductions. To ensure precautionary management (38) we applied  $F$  levels corresponding to a  $<5\%$  risk of population decline below ecologically safe levels. By adopting this strategy, we initialized the simulations in 1991 and 1992, the years after the collapse below  $B_{pa}$  and  $B_{lim}$ , and managed the stock forward until 2004. By running 1,000 stochastic simulations, we show that our precautionary management strategy, by adapting fishing pressure to environmental conditions and food-web interactions, could significantly have prevented the cod stock from collapsing and promoted a stock recovery above ecologically safe levels (Fig. 3 B and D).

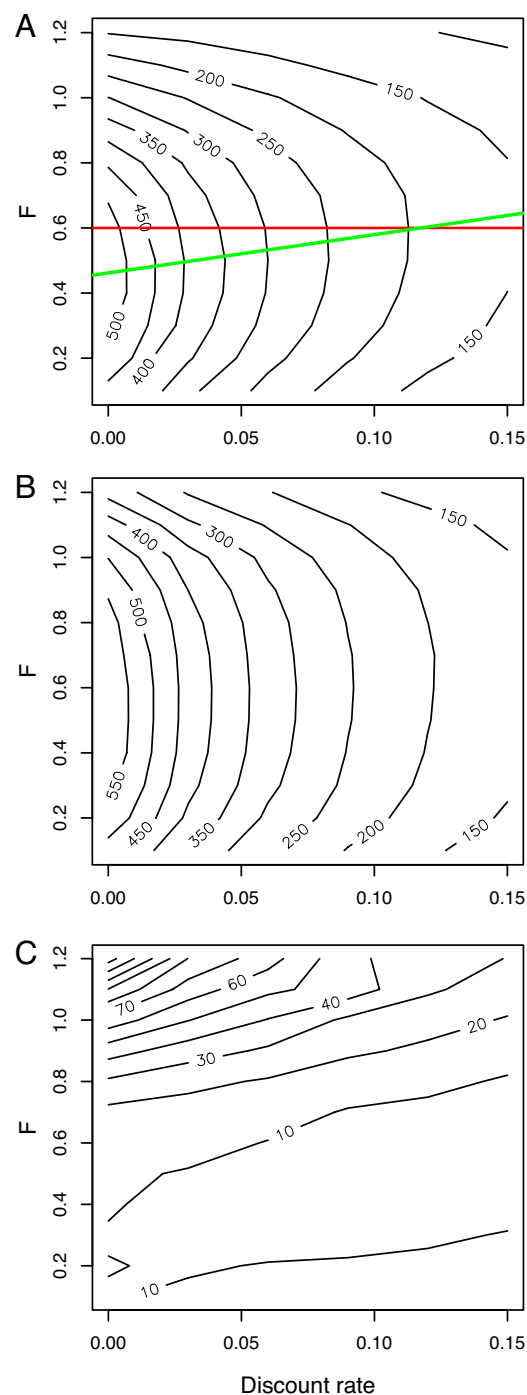
Additionally, to demonstrate that our adaptive management strategy is essential in preventing future stock collapses we simulated a set of long-term dynamics of Baltic cod under three different management scenarios: (i) fishing mortalities fluctuate at mean historical levels (1974–2004); (ii) fishing mortalities remain fixed at  $F_{pa} = 0.6$ ; and (iii) fishing levels are adapted to salinity conditions (i.e.,  $F$  varies according to  $0.6 \pm 0.3$ ). Forced under the same environmental scenario (i.e., resembling the historical range of fluctuations in SST and salinity conditions) only the adaptive management approach may prevent future stock collapses and maintain the stock stably above ecologically





**Fig. 4.** Simulated long-term dynamics of Baltic cod under different management scenarios. (A) Fishing mortalities fluctuate at mean historical levels. (B) Fishing mortalities are fixed at  $F_{pa}$  (0.6). (C) Fishing levels are adapted to salinity conditions (i.e.,  $F = 0.6 \pm 0.3$ ). To resemble the historical range of fluctuations in SST and salinity, environmental conditions were simulated based on the mean, variance, and autocorrelation structure of the observed time series (1974–2004) using an approach for modeling “red-shifted,” i.e., positively autocorrelated marine environments (39, 40). Simulations were initialized at the mean historical SSB levels for each species and replicated 1,000 times including stochastic process noise. Solid horizontal lines mark the recommended ecologically safe levels of Baltic cod, the precautionary stock level,  $B_{pa}$  (green), and limiting stock level,  $B_{lim}$  (red). Black contour lines show the 90% and 95% prediction intervals within which the cod stock dynamics of each replicated run fluctuates.

sustainable levels,  $B_{pa}$  and  $B_{lim}$  (Fig. 4C). Although the fixed reference approach may reduce large-scale variability in SSB (Fig. 4B) compared with a more “random” harvesting scenario



**Fig. 5.** Economic revenue (m€) of the Baltic cod fishery. (A and B) Revenue is shown under a fixed (A) and adaptive management (B) strategy. NPVs are shown over a range of fishermen discount rates (0–15%) and fishing mortalities ( $F$  from 0 to 1.2). Fishing mortalities for sprat and herring are maintained at mean historical levels. (C) The net revenues (i.e., the percentage difference between the adaptive and fixed management scenario) are shown. The economically optimal exploitation levels ( $F_{opt}$ ) is shown in green, and the horizontal red line marks the precautionary fishing mortality,  $F_{pa}$ .

(Fig. 4A), it does not sufficiently buffer against climate-driven recruitment failure nor prevent recurrent stock collapses.

### Bio-Economic Scenarios

In an effort to adopt a holistic management perspective we finally coupled the food-web model to a simple bio-economic



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# Supporting Information

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## SI Text

**Model Fitting and Selection.** In fitting the MAR(1) food-web model, we used data on SSB of cod, sprat, and herring from 1974 to 2004 derived from multispecies stock assessment (MSVPA) in the Baltic Sea (1). Model fitting was performed separately on both log-transformed and normalized SSB values. To include the top-down effect of commercial fishing on the dynamics of the three species, time series on mean annual fishing mortality ( $F$ ) of cod, sprat, and herring were used as covariates. Further, to encompass environmental and zooplankton effects, abiotic and biotic variables known to affect recruitment of cod, sprat, and herring were included (Table S1). To take into account any geographical differences in hydrographic forcing (2), environmental variables were taken separately from the two main subbasins of the Central Baltic Sea, the southern Bornholm Basin and the northern Gotland Basin. Egg and larval survival of Central Baltic cod is affected mainly by salinity and oxygen conditions in the deep Baltic basins (3). The effect works directly on the eggs (4), but also indirectly on the availability of the copepod *P. acuspes* (5), the main food source for larval cod. Furthermore, *P. acuspes* is the dominant prey for herring (6). To address both these effects, we included salinity and oxygen concentration in the deepwater and  $\ln(x + 1)$ -transformed biomass of *P. acuspes* as potential covariates. We further used the reproductive volume (i.e., the water volume with a salinity  $>11$  psu and an oxygen content  $>2 \text{ mL} \cdot \text{L}^{-1}$ ) representing the minimal conditions for successful cod egg development in the deep Baltic basins (7). Temperature is the main environmental variable influencing sprat recruitment (8) by directly affecting egg and larval survival (4). Indirectly temperature affects the production and hence the availability of the copepods *Acartia* spp (6), which are important for the survival of larval sprat (9). Thus, we included both temperature and  $\ln(x + 1)$ -transformed biomass of *Acartia* spp. as potential covariates in the analysis. Hansson et al. (10) argue that eutrophication has a strong impact on the Baltic ecosystem, because enhanced primary production increases total fish production but at the same time it may induce hypoxia in bottom waters. To account for this effect, we used  $\ln(x + 1)$ -transformed values of spring and summer chlorophyll (*a* Chl. *a*) in the analysis. Finally, the Baltic Sea Index (BSI) was included because it reflects the impact of climate variability on oceanographic processes in the area (11).

To avoid colinearity between environmental and zooplankton covariates, we included only one abiotic and biotic variable per species in the full model. Before model reduction the full model was therefore fitted with each covariate separately and at different time lags (1–3 years). The time lags aim to represent the period until recruitment of the species to the fisheries. The covariates included in the full model were then chosen based on the significance level of the parameters (Table S1). Then by stepwise model reduction, the full model was penalized for complexity. We minimized the negative log-likelihood function and applied the likelihood ratio test to compare full and reduced models (Table S2).

**Model Diagnostics.** A number of diagnostics were applied to assess whether the final MAR(1) model gave a reasonable description of the food-web dynamics. The assumption of normality of the error terms is supported by an analysis of the residuals (Fig. S1). A partial autocorrelation analysis of the residuals further indicates that the model errors were independent for all species and lags, the only exception being a slight autocorrelation in the fifth- and sixth-year lag for sprat and cod, respectively (Fig. S1). Both  $R^2$  values and conditional  $R^2$  values, reporting the proportion of

change from  $t$  to  $t + 1$  show a high degree of explained variance for all species (Table S3). Finally, a stability analysis of the final parameters of the community matrix reveals a dominant eigenvalue below one ( $\lambda_1 = 0.93$ ) (Table S5), indicating a stable, stationary food web (12, 13). Our model thus has captured the essential dynamics of a natural, stable system. The log-transformed version of the model showed a considerably lower degree of conditional explained variance and marked autocorrelation in the residuals compared with the normalized version. The subsequent simulations were therefore based only on the normalized version.

**Model Validation.** A way of validating the predictive capabilities of a model is to fit on a subset of the available data and then check the model by forecasting the remainder of the data (14). Therefore, we adopted a sequential refitting procedure where the model was initially fitted to only the first 10 years of the dataset and then refitted on a yearly basis, producing a prediction for each consecutive year. The predicted values and associated 95% prediction intervals were compared with the observed values to assess the predictive accuracy of the model. The sequential refitting procedure serves a purpose not only to validate the model but as a realistic stock assessment tool, where we in retrospect forecast the future stock size to give sound management advice for the coming year. Additionally, the food-web dynamics was simulated by using only the first-year values as initial conditions. This procedure is fundamentally different from a simple fit to the data, because the observed values from the second year onward are not used (15). Simulations were run 1,000 times with random process noise added at each time step. Mean values and a 95% confidence interval of the predictions were computed. To assess the relative contribution of environmental and species interactions in affecting the food-web dynamics, we performed an additional hindcast simulation by using a simpler single-species MAR(1) model fitted only to fishing mortalities and biomasses of each individual species separately. Both the sequential refitting and the simulated dynamics demonstrated a distinct ability to “recreate the past” dynamics of cod, herring, and sprat (Fig. S2). The hindcast simulations without accounting for environmental forcing and species interactions, however, did not at all explain nor recreate the past dynamics of the three species, especially in the case of cod and sprat (Fig. S2). All statistical analysis were conducted with R software ([www.r-project.org](http://www.r-project.org)).

**Model Simulations.** To compare alternative management strategies we estimated the mean annual yield of the Baltic cod fishery and the probability of stock decline below  $B_{\text{lim}}$  given a fixed- and adaptive management scenario. In the fixed scenario, reference levels ( $F$ ) remain fixed in the range from 0.3 to 1.0, whereas in the adaptive scenario we allow  $F$  levels to additionally vary with  $\pm 0.3$  dependent on climate conditions (i.e., hence  $F$  0–0.6 and 0.6–1.2 corresponds to the lowest and highest adaptive exploitation pressure, respectively). Furthermore, to study yield curves and probabilities during variable climate we performed multiple stochastic simulations over a range of salinity levels corresponding to the observed fluctuations in salinity from 1974 to 2004.

In both the fixed and adaptive scenarios mean annual yield (Kt) increase with salinity levels, reflecting the increased input of recruits to the fishable stock caused by enhanced egg and larvae survival (3) (Fig. S3 *a* and *b*). On average, the adaptive

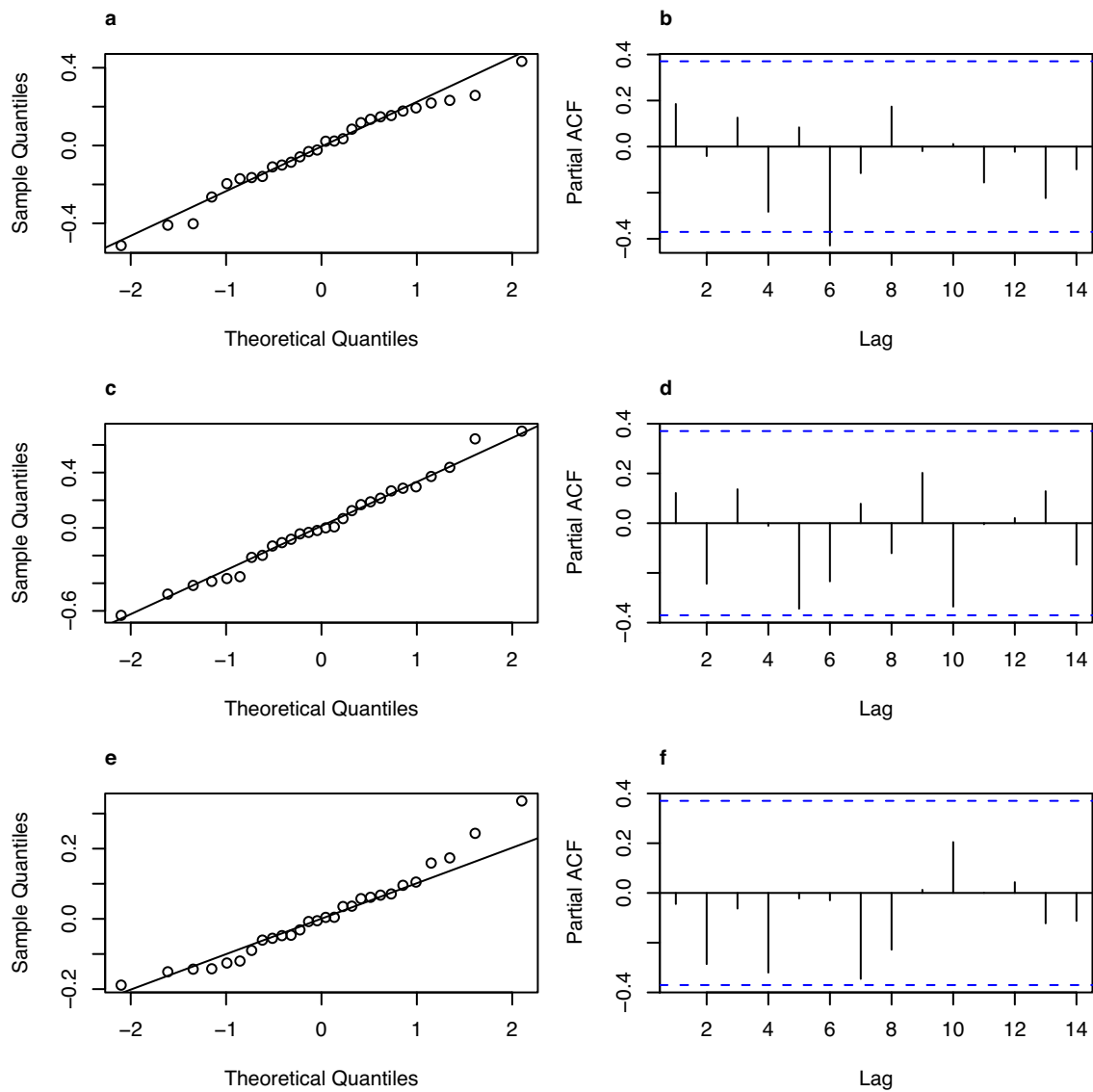


scenario gives higher yields as it guarantees stock biomass to remain at higher mean levels compared with the fixed approach (Fig. 4). Given an adaptive approach we can show how under highly unfavorable salinity conditions the adaptive approach allows for a yield  $\approx 3$ –4 times the fixed yield (i.e.,  $\approx 35$  and  $<10$  Kt). During favorable salinity conditions for spawning and recruitment, however, the difference in mean yield decreases,

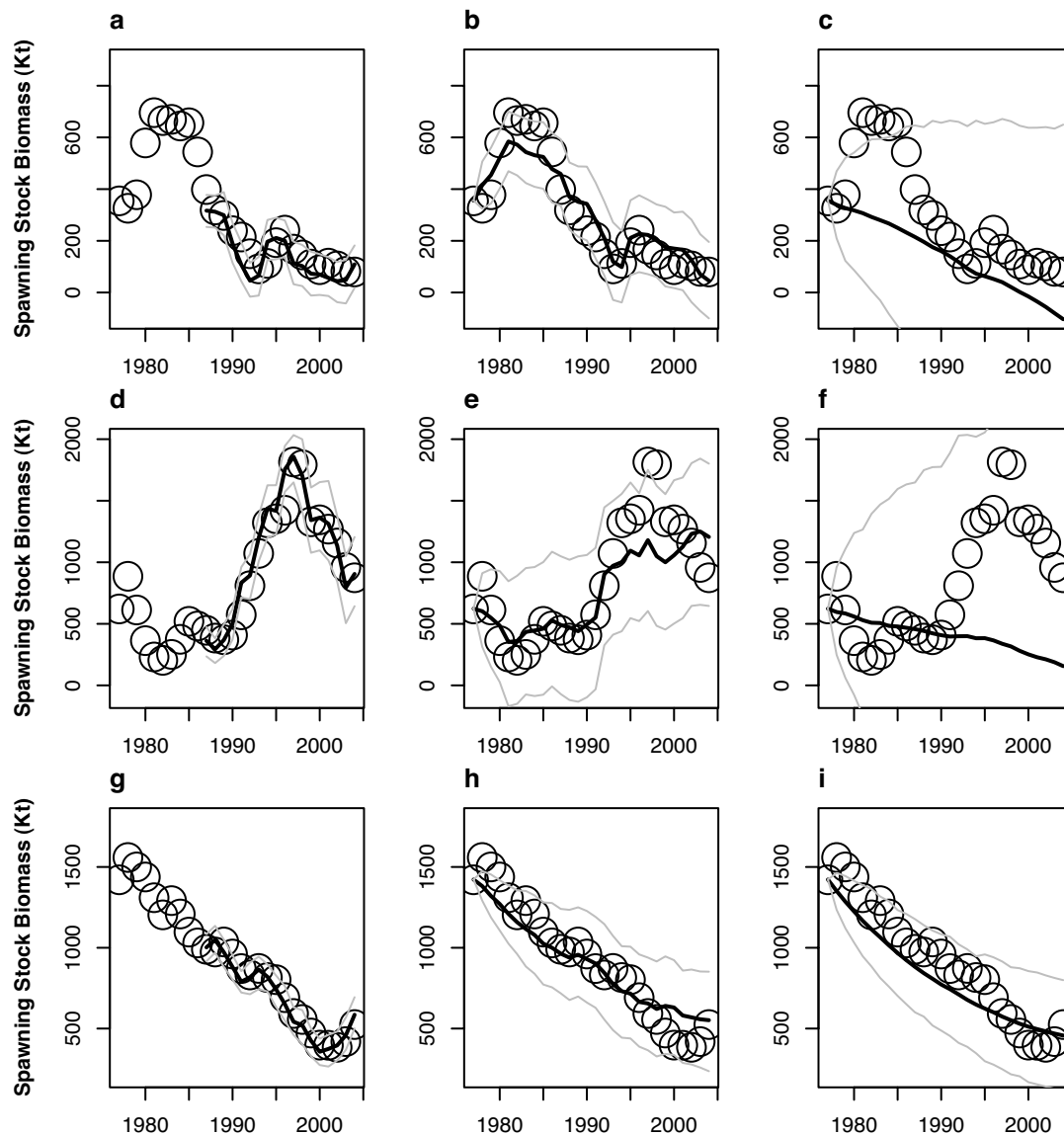
illustrated by an adaptive and fixed yield of  $\approx 120$  and  $\approx 90$  Kt, respectively. Finally, concerning the probability of collapse below  $B_{lim}$  the adaptive approach (Fig. 3d) by buffering against climate variability considerably reduces the risk of future stock collapse compared with a fixed strategy (Fig. 3c), despite equal mean  $F$  levels.

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**Fig. S1.** Model diagnostics. Normal probability plots (a, c, and e) and partial autocorrelation coefficients (b, d, and f) of residuals for cod (a and b), sprat (c and d), and herring (e and f) from the final MAR(1) model.



**Fig. S2.** Model validation through hindcasting. Observed (open circles) and simulated biomass (solid lines) of Baltic cod (a–c), sprat (b–f), and herring (g–i) from 1977 to 2004, showing the MAR(1) model’s ability to recreate the food-web dynamics. (a, d, and g) Yearly predictions from the sequential refitting approach, where the model was initially fit to only the first 10 years and for each following year it was refitted. (b, e, and h) The results from simulations using only the first-year values in 1977 as initial conditions are shown. Simulations were replicated 1,000 times (each time with random process noise added). (c, f, and i) Simulations from a model fitted only to fishing mortalities and biomasses for each species separately are shown. Gray lines indicate the upper and lower 95% confidence intervals of the simulations.



**Table S1. Covariates and parameter *P* values from the full model fitting**

Covariate	Cod	Herring	Sprat
Spring temperature (0–10 m) GB	0.69	0.91	0.007**
Spring temperature (40–60 m) GB	0.86	0.21	0.008**
Summer temperature (0–10 m) GB	0.54	0.18	0.15
Summer temperature (40–60 m) GB	0.62	0.84	0.04*
Spring temperature (0–10 m) BB	0.48	0.13	0.30
Spring temperature (40–60 m) BB	0.53	0.30	0.08
Summer temperature (0–10 m) BB	0.33	0.30	0.01*
Spring salinity (0–10 m) GB	0.16	0.06	0.04*
Spring salinity (80–100 m) GB	0.05*	0.15	0.21
Summer salinity (0–10 m) GB	0.12	0.05*	0.04*
Summer salinity (80–100 m) GB	0.05*	0.04*	0.32
Spring salinity (0–10 m) BB	0.30	0.11	0.04*
Spring salinity (70–90 m) BB	0.18	0.21	0.01*
Winter bottom oxygen BB	0.56	0.16	0.49
Winter bottom oxygen GB	0.68	0.39	0.90
Reproductive volume	0.06	—	—
Baltic Sea Index (BSI)	0.11	0.62	0.08
Spring <i>Acartia</i> spp. GB	—	—	0.007**
Summer <i>Acartia</i> spp. GB	—	—	0.07
Spring <i>Pseudocalanus</i> spp. GB	0.66	0.68	—
Summer <i>Pseudocalanus</i> spp. GB	0.17	0.01*	—
Spring [Chl. a] BB	0.31	0.41	0.49
Summer [Chl. a] BB	0.30	0.87	0.22
Spring [Chl. a] GB	0.52	0.48	0.78
Summer [Chl. a] GB	0.70	0.18	0.88

Climate variables are taken from the Gotland Basin (GB) and the Bornholm Basin (BB) separately. The bold values show the most significant climate and zooplankton variables chosen to be included in the full model. The variable for cod is lagged by 3 years, whereas the variables for sprat and herring are lagged by 1 year.

**Table S2. Model reduction**

Eq.1	$-\log(L)$	$P$ value	$R^2$	Conditional $R^2$
Full model	−15.66		[0.96, 0.90, 0.98]	[0.57, 0.39, 0.55]
Cod:zooplankton	−15.66	0.99	—	—
Sprat:zooplankton	−14.90	0.47	—	—
Cod:sprat	−14.53	0.52	—	—
Sprat:herring	−14.52	0.69	—	—
Herring:salinity	−12.05	0.21	[0.95, 0.89, 0.98]	[0.56, 0.36, 0.53]

Final model evaluation using negative log likelihood estimation and the likelihood ratio test for model reduction. The total and conditional explained variance for cod, sprat, and herring are shown for the full and the final models only.  $P > 0.05$  indicate that the complex model does not fit the data significantly better than the reduced model. The parameter can thus be excluded.

**Table S3. Fit of the model for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004**

Variate	Total $R^2$	Conditional $R^2$
Cod	0.95	0.56
Sprat	0.89	0.36
Herring	0.98	0.53

Table S4. Parameter estimates for species interactions, the community matrix for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004

	Cod	Sprat	Herring
Cod	0.67 [0.55, 0.80]	0	0.23 [0.08, 0.37]
Sprat	−0.06 [−0.12, 0.00]	0.90 [0.73, 1.06]	0
Herring	−0.09 [−0.16, −0.02]	−0.10 [−0.19, −0.02]	0.87 [0.77, 0.97]

**Table S5. Eigenvalue analysis of the community matrix for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004**

Variate	Eigenvalue
Cod	$0.93 + 0.00i$
Sprat	$0.76 + 0.13i$
Herring	$0.76 - 0.13i$



**Table S6. Parameter estimates with 95% confidence intervals for covariates, fishing, climate, and zooplankton for the final MAR(1) model fitted to Baltic Sea time series data from 1974 to 2004**

Variate	Fishing	Climate	Zooplankton
Cod	−0.91 [−1.31, −0.52]	0.08 [0.02, 0.14]	0
Sprat	−0.34 [−1.20, 0.51]	0.08 [0.04, 0.13]	0
Herring	−0.82 [−2.14, 0.51]	0	0.15 [0.05, 0.26]



## Ecological forecasting under Climate Change – the case of Baltic cod

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### ABSTRACT

Good decision making for fisheries and marine ecosystems requires a capacity to anticipate the consequences of management under different scenarios of climate change. The necessary ecological forecasting calls for ecosystem-based models capable of integrating multiple drivers across trophic levels and properly including uncertainty. The methodology presented here assesses the combined impacts of climate and fishing on marine food-web dynamics and provides estimates of the confidence envelope of the forecasts. It is applied to cod (*Gadus morhua*) in the Baltic Sea, which is vulnerable to climate-related decline in salinity due to both direct and indirect effects (i.e., through species interactions) on early-life survival. A stochastic food web-model driven by regional climate scenarios is used to produce quantitative forecasts of cod dynamics in the 21<sup>st</sup> century. The forecasts show how exploitation would have to be adjusted in order to achieve sustainable management under different climate scenarios.

## 1. INTRODUCTION

Ecosystems worldwide have already shown clear evidence of change in response to global warming (Walther *et al.* 2002; IPCC 2007; Rosenzweig *et al.* 2008). Since ecosystems provide vital goods and services, our ability to anticipate future changes is of great concern. In order to be of value in decision making and management, ecological forecasts should explicitly account for uncertainties and provide quantitative assessments of the risks associated with management actions (Clark *et al.* 2001). Forecasting in agriculture and forestry is today fairly well developed (Easterling & Apps 2005), based on a long tradition of large scale experimentation and modelling (Adams *et al.* 1990; Joyce *et al.* 1995), however many ecological models ignore key sources of uncertainty, thereby providing incomplete information for evaluating risk (Clark *et al.* 2001). Although large uncertainty should not impede efforts to anticipate change, difficulties in evaluating impacts of climate change on marine ecosystems have resulted in a lack of reliable forecasts for fisheries production (Brander 2007). By adopting holistic ecosystem-based approaches, which consider both internal and external drivers (Pikitch *et al.* 2004; deYoung *et al.* 2004) we can include many sources of uncertainty and provide quantitative risk assessments for future fisheries production under different climate and fisheries management scenarios.

Atlantic cod is among the commercially most important fish species in the North Atlantic. Many of the stocks have collapsed due to the joint effects of overfishing (Myers *et al.* 1997; Hutchings 2000; Frank *et al.* 2005) and climate driven declines in productivity (Beaugrand *et al.* 2003; Lilly *et al.* 2008). Several studies have set out scenarios for cod stocks in the North Atlantic (Drinkwater 2005) and Baltic Sea (MacKenzie *et al.* 2007) based on global and regional climate projections. However these are qualitative scenarios which do not provide the information to assess risk from the joint effects of exploitation and environmental change (Clark *et al.* 2001). In order to provide quantitative risk assessments ecosystem-based models capable of integrating multiple drivers across trophic levels and properly including uncertainty are essentially needed (Clark *et al.* 2001; deYoung *et al.* 2004). Statistical models have proven useful in incorporating key ecological and environmental drivers and evaluating multiple sources of uncertainty (Walter *et al.* 1986; Harwood & Stokes 2003; Hjermann *et al.* 2004). We used the BALMAR food-web model (Lindegren *et al.* 2009) integrating species interactions, between cod and the forage fish

species herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) with external forcing through fishing, zooplankton and climate (supplementary figure 1) to assess the risks of future stock collapse under different climate scenarios. Coupled with a climate model we were able to address the main external and internal sources of uncertainty (figure 1) and provide not only quantitative forecasts for Baltic cod but advice for achieving sustainable fisheries in the 21<sup>st</sup> century.

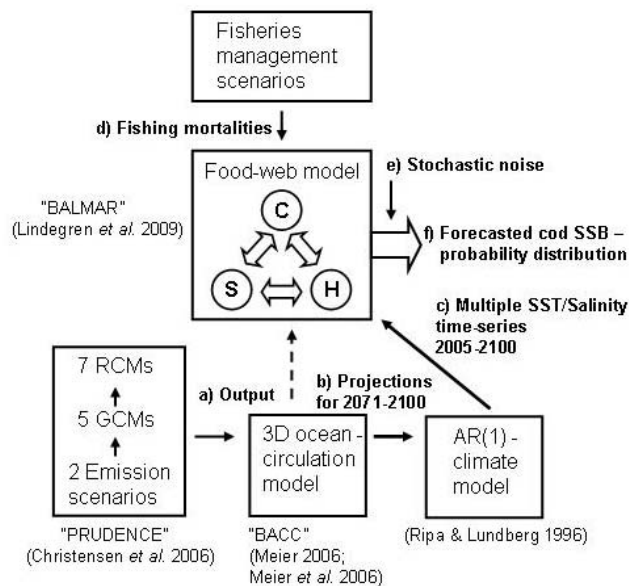


Figure 1. A coupled food web-climate model approach to forecasting Baltic cod stock dynamics in the 21<sup>st</sup> century. The BACC assessment use a 3D ocean circulation model to explore the range of projected climate changes in the Baltic Sea region based on climate scenarios from the PRUDENCE ensemble model,. The BACC assessment conducted “time-slice” simulations for 2071-2100 but no transient time-series are available. In order to facilitate coupling with the food-web model, an AR(1)-climate model was used to simulate transient time-series based on the future projections for each variable. Additionally, multiple simulations were run in order to represent the variability and uncertainty in climate forcing in the 21<sup>st</sup> century. Finally, the response of the cod stock to climate and fisheries management was studied by forcing the food-web model with fishing mortalities for cod (C) as well as for sprat (S) and herring (H). Cod stocks dynamics are forecasted as a 95% probability distribution of future SSB by running multiple stochastic simulations including random noise.

## 2. MATERIAL AND METHODS

### (a) *The Climate model*

We base our climate forecasts on simulation outputs from the BALTEX Assessment of Climate Change for the Baltic Sea Region (BACC 2007). It applies a multi-model ensemble

approach (developed by the PRUDENCE project; Christensen *et al.* 2007) based upon seven regional circulation models, five global circulation models, and two emission scenarios to explore the range of outcomes and to enhance confidence in projected climate changes in the Baltic Sea (Meier 2006; Meier *et al.* 2006). This approach takes into account projections for precipitation and run-off, causing a freshening (i.e., decreasing salinities) of the Baltic Sea, as well as the effect of wind-driven inflows of high-saline water from the North Sea. Existing projections for 2071-2100 do not include transient time series for different seasons, areas and depths (Meier 2006). Therefore, we simulated future time series representing not only the projected change but the uncertainty and variability in climate forcing during the coming 100 years using an AR(1) climate model (Ripa & Lundberg 1996). We generated “red-shifted” transient time series (Steele & Henderson 1984) ( $\Phi_{t+1}$ ) for spring sea surface temperature (SST) and summer salinity (80-100m) of the Gotland Basin (i.e., the largest and northernmost spawning area of cod in the Baltic Sea):

$$\phi(t+1) = \alpha\phi(t) + \beta\varepsilon(t+1) \quad (1)$$

where  $\varepsilon_t$  is random “white” noise (zero mean and unit variance),  $\beta$  a parameter specifying the degree of environmental variation and  $\alpha$  a measure of the autocorrelation in the time series. The degree of autocorrelation was estimated by fitting an autoregressive time series model to the observed SST and salinity data from 1974-2004, where the  $\alpha$  parameter corresponds to the first-order autoregression coefficient. In the case of salinity, a marked “red-shifted” dynamics was found, i.e., autocorrelation ( $\alpha = 0.66$ ) was significantly larger than zero (which corresponds to uncorrelated “white” noise). The strong degree of autocorrelation is due to the relatively low inter-annual variability in bottom salinity conditions in the Baltic Sea. In contrast, the strong and rapid fluctuations in SST give rise to a lower degree of autocorrelation ( $\alpha = 0.21$ ).

The future series (from 2005-2104) were simulated based on the actual mean, variance ( $\beta$ ) and autocorrelation ( $\alpha$ ) of the observed time series from 1974-2004. To simulate the predicted increase in Baltic Sea SST by 3.5°C and decrease in salinity by 0.8 or 4.8 psu, i.e., dependent on the choice of global circulation model (Meier *et al.* 2006; BACC 2007; supplementary figure 2b-c), a gradual trend in the mean over 100 consecutive years was added. We also simulated future climate time-series over a large spectrum of environmental

autocorrelation (i.e.,  $\alpha = 0$  to 1) because of concerns that global climate change may influence population persistence through changes also in the autocorrelation structure of the environment (Wigley *et al.* 1998; Pounds *et al.* 1999). Although species responses may change from a positive to a negative over wide ranges in temperature (MacKenzie *et al.* 2004), we assume that the responses of Baltic cod to salinity and sprat to temperature remain positive, at least within the relatively narrow ranges predicted here (MacKenzie & 2004; Köster *et al.* 2005). Using these simulations as inputs, we forced our food web model bottom-up (figure 1), exploring the impact of climate change on the future dynamics of Baltic cod, sprat and herring. Since herring was not directly forced by climate, but rather indirectly through its main prey, *Pseudocalanus acuspes* (Möllmann *et al.* 2003; Voss *et al.* 2003), we simulated the climate effect as an indirect linear response to salinity mediated by *Pseudocalanus acuspes* (Salinity-*Pseudocalanus acuspes*:  $r = 0.65$ ,  $n = 26$ ).

#### (b) *The Food-web model*

We studied the dynamics of Baltic cod, sprat and herring using the BALMAR food-web model (Lindgren *et al.* 2009), a linear state-space model based on a theoretical approach for predicting long-term responses of populations to environmental change (Ives 1995; Ives *et al.* 2003). The approach, a first-order multivariate autoregressive model (MAR(1)) applies a statistical framework for modelling food-web interactions at multiple trophic levels (Ives *et al.* 2003) and essentially functions as a set of lagged multiple linear regression equations (one for each species of the food web) solved simultaneously to arrive at the most parsimonious model overall (Hampton & Schindler 2006). Written in state-space form, the MAR(1) model we used is given by:

$$\mathbf{X}(t) = \mathbf{B}\mathbf{X}(t-1) + \mathbf{C}\mathbf{U}(t-y) + \mathbf{E}(t) \quad (2)$$

$$\mathbf{Y}(t) = \mathbf{Z}\mathbf{X}(t) + \mathbf{V}(t) \quad (3)$$

where  $\mathbf{X}$  are spawning stock biomasses (SSB) of cod, sprat and herring derived from multi-species stock assessment (MSVPA) in the Baltic Sea at time  $t$  and  $t-1$  respectively and  $\mathbf{B}$  is a  $3 \times 3$  matrix of species interactions, an analogue of the “community matrix” used in food-web theory (May 1972; Pimm 1982). The covariate vector  $\mathbf{U}$  represents the effects of commercial fishing, climate and zooplankton and contains lagged values of mean annual fishing mortalities ( $F$ ) and a number of selected climate and zooplankton variables known

to affect recruitment of cod, sprat and herring respectively.  $C$  is a  $3 \times 9$  matrix whose diagonal elements specify the effect of covariates (i.e., fishing, climate and zooplankton) on each species. The process error  $E(t)$  is assumed multivariate normal and temporally uncorrelated. Likewise, the observation error of the covariance matrix of the normal random variable  $V(t)$  is assumed independent. Regression parameters were found by maximum likelihood estimation using a Kalman filter (Harvey 1989). The Kalman filter is a recursive estimator that sequentially calculates the unobserved SSB values  $X(t)$  from the previous time step ( $t-1$ ) using the model formula specified in Eq. 2. Predictions from the “hidden” state are then updated using the actual observed SSB values,  $Y(t)$  of the “true” observed state (Eq. 3). Model fitting was performed on time series covering the period 1974-2004. Finally, the most parsimonious model in terms of the number of parameters and the explained variance was selected and validated (Lindegren *et al.* 2009).

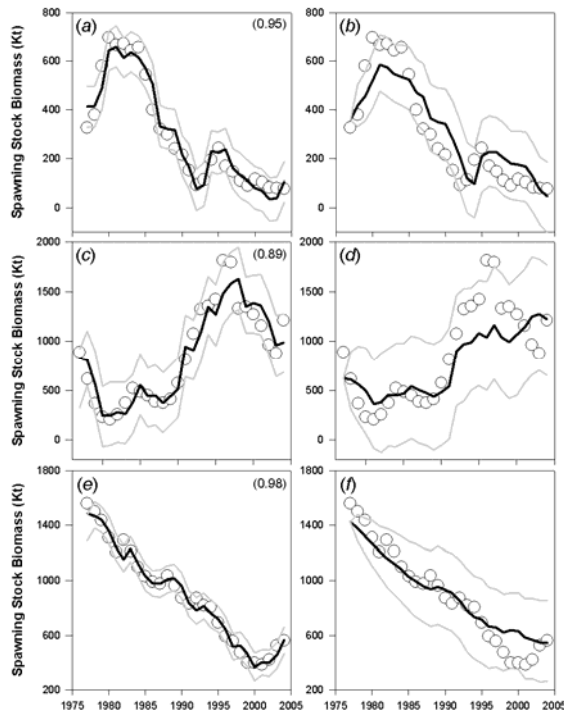


Figure 2. Model validation by means of fitting and hindcasting the historical stock dynamics of Baltic cod (*a-b*), sprat (*c-d*) and herring (*e-f*). The left column show the fit of the BALMAR food-web model (Lindegren *et al.* 2009), where SSB levels (black) accurately represent the observed dynamics (circles) of cod, sprat and herring from 1977 to 2004. (The degree of explained variance is shown in parenthesis). The right column demonstrates hindcast SSB levels (black), where the historical stock dynamics were simulated based only on the starting biomasses (i.e., in 1977) as initial conditions. Grey lines are upper and lower 95% prediction intervals.

The final BALMAR model accurately captured the known mechanisms of species interactions within the Baltic Sea food-web (table 1; supplementary figure 1), e.g., density-dependence/cannibalism (Sparholt 1994; Köster & Möllmann 2000; Neuenfeldt & Köster 2000), competition (Möllmann *et al.* 2005) and predation (Sparholt 1994). The model



parameters also illustrate the negative effect of commercial fishing and the positive effect of zooplankton and climate (as represented by SST and salinity conditions) on growth, survival and recruitment of cod (Köster *et al.* 2005), sprat (MacKenzie & Köster 2004) and herring (Möllmann *et al.* 2005) respectively. The fitted model reproduced well the historical fish stock dynamics in the Baltic Sea (Figure 2a, c, e). These are characterized by the collapse of the cod stock from high levels during the early 1980s, the large increase of the sprat stock since the late 1980s, and a constant decline of herring biomass. Furthermore, the food-web dynamics was simulated using only the first year SSB values as initial conditions (figure 2b, d, f). This procedure is fundamentally different from a simple fit to the data, as the observed values from the second year onwards are not used (Hjermann *et al.* 2004). The ability of the model to accurately recreate the past response of the fish community to climate and fisheries is a necessary basis for studying the effects of future changes in climate and fisheries management. All statistical analyses were conducted using the R software ([www.r-project.org](http://www.r-project.org)).

### **(c) Future climate and management scenarios**

In order to study the effects of climate change on Baltic cod, we used a coupled climate–food web model approach (figure 1) in simulating four future scenarios for the Baltic Sea (a-d). Due to large uncertainties in regional climate forecasting (Meier *et al.* 2006; BACC 2007) (supplementary figure 2) these scenarios aim to illustrate a number of probable “what if”- scenarios. Furthermore, the simulations apply a number of fishing strategies to study the role of fisheries management. In the first scenario (a), we provide a “control scenario” where climate (SST and salinity) and fishing mortalities are kept at mean historical levels ( $F = 0.91$ ; 1974-2004). In the second scenario (b), climate change is introduced by simulating an increasing trend in SST by  $3.5^{\circ}\text{C}$  and decreasing trend in salinity by 4.8 psu. Fishing mortalities however remain fixed at mean historical levels. In (c), the same climate change is combined with a reduction in cod fishing mortalities to the previously recommended precautionary fishing mortality ( $F_{\text{pa}} = 0.6$ ). The final scenario (d) simulates climate change with the same increase in SST by  $3.5^{\circ}\text{C}$  but with a smaller decrease in salinity by only 0.8 psu. Fishing mortalities remain at  $F_{\text{pa}}$ . For each scenario (a-d), we performed 1000 replicated stochastic simulations (supplementary figure 3). At each time step process noise was added to account for the main sources of uncertainty not covered by

variability in climate, fishing or species interactions. By choosing a structurally simple model we acknowledge that we may not specifically address future variability stemming from (i) changes in species composition, e.g., due to invasive species, (ii) changes in species distribution, (iii) drastic changes in ocean productivity or (iv) other anthropogenic disturbances (e.g., oil spills etc). Bearing in mind that these possible additional sources of variability are not included, the response of cod spawning stock biomass (SSB) to future scenarios (a-d) is presented as a 95% probability distribution for each scenario.

#### **(d) *Adaptive management under climate change***

In order to investigate the synergistic effects of climate and fishing (Ottersen *et al.* 2006; Anderson *et al.* 2008) and derive sustainable exploitation levels for Baltic cod under different scenarios of climate change, we ran multiple simulations for each combination of salinity (i.e., projected decrease from 0 – 5 psu) and fishing (F from 0-1), keeping the projected increase in SST fixed at 3.5 °C. The cod stock response was computed as the percentage of simulations where SSB drops below the limiting stock level ( $B_{lim} = 160$  Kt), hence a measure of the probability of stock collapse below ecologically safe levels. Given the concern that global climate change may influence population persistence through changes in the autocorrelation structure of the environment (Wigley *et al.* 1998), we additionally estimated the probability of stock collapse over a large spectrum of environmental autocorrelation (i.e.,  $\alpha = 0$  to 1) with the projected increase in SST and salinity fixed at 3.5 °C and 0.8 psu respectively.

### **3. RESULTS AND DISCUSSION**

#### **(a) *Ecological forecasting***

Since the credibility of our forecasts depends in part on the ability to accurately recreate the past response of the fish community to climate and fisheries, we initiated our simulations in 1977 and forced the model by the observed climate and F levels until 2007. Despite slight underestimation at high stock levels and overestimation at low levels, the observed values were all within the confidence limits of the predictions (figure 3). Based on this demonstrated ability to hindcast the past dynamics, we projected the response of cod to four future scenarios which include changes in both climate and fisheries management.

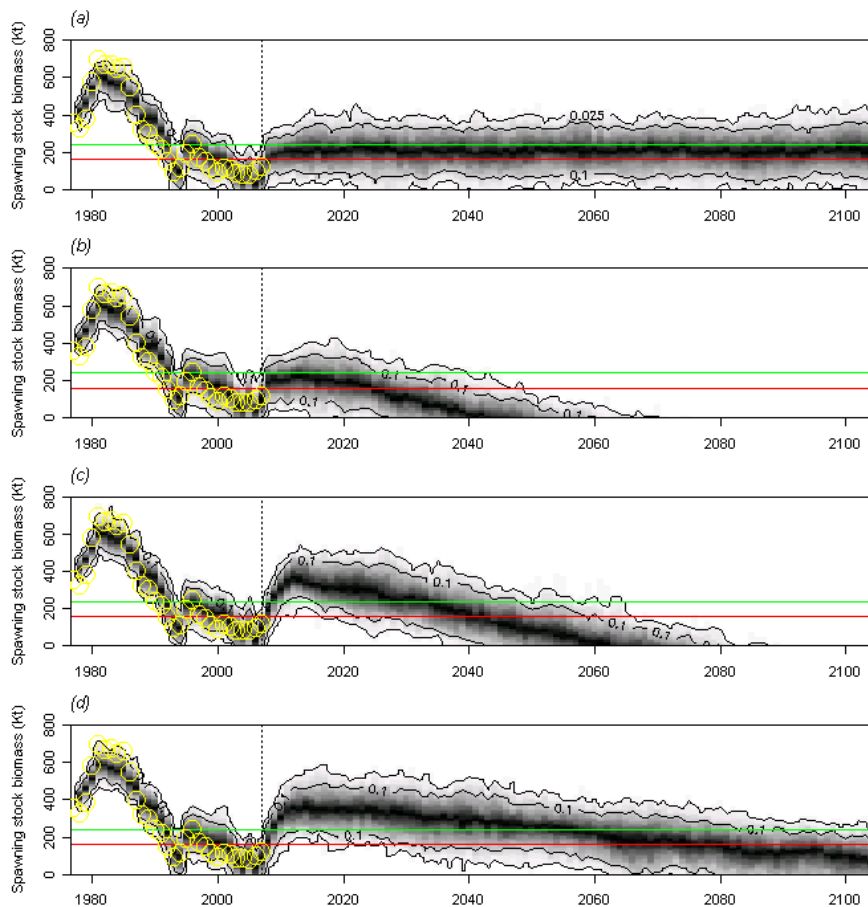


Figure 3. Future climate and management scenarios and a 95% probability distribution of Baltic cod SSB. (a) A “control scenario” where climate (SST and salinity) and fishing mortalities (F) fluctuate at mean 1974-2004 levels. Hindcasted simulations from 1977-2007 (i.e., based on the observed climate and F levels for these years) are compared with observed SSB (yellow circles) to validate the predictive accuracy of the model. (b) A predicted increase in mean SST by 3.5°C and decrease in mean salinity by 4.8 psu combined with mean F levels. (c) As in (b) but with F reduced to the previously recommended precautionary reference levels ( $F_{pa}$ ). (d) Exploitation at  $F_{pa}$  but with a predicted decrease in salinity by only 0.8 psu. Solid horizontal lines mark the recommended ecologically levels of Baltic cod, the precautionary stock level,  $B_{pa}$  (green) and limiting stock level,  $B_{lim}$  (red). (Note that the use of these biomass reference points is currently being re-evaluated). Black contour lines show the 90% and 95% prediction intervals within which the cod stock dynamics of each replicated run fluctuates.

The first “control scenario” without changes in climate and at mean historical F levels (1974-2004), predicts an initial increase and future mean biomass fluctuating slightly below the so-called precautionary stock level ( $B_{pa}$ ) but above the limiting stock level ( $B_{lim}$ ) (figure 3a). The initial increase in biomass, which is predicted in all four scenarios, is in accordance with recent observed dynamics as well as short-term stock assessment forecasts

(ICES 2007) and is due to improved salinity and oxygen conditions following inflow events from the North Sea (e.g., in 2003), combined with recent reductions in fishing mortalities. Due to stochasticity in climate and process noise, the lower 95% prediction interval however is close to zero, indicating a small probability ( $< 2.5\%$ ) of extinction even without climate change. This probability increases if we add the slight tendency to overestimate biomass at low stock levels. Thus even if the mean climate does not change, current fishing mortality must be kept low in order to reduce the risk of extinction. In the second scenario (figure 3*b*), a combination of long-term change in SST ( $+3.5\text{ }^{\circ}\text{C}$ ) and salinity ( $-4.8\text{ psu}$ ) with mean  $F$  levels results in a forecast of initial stock recovery followed by a gradual decrease and probable extinction ( $>95\%$ ) of cod by mid-2060s. The extinction is due to climate driven recruitment failure combined with high fishing pressure. The third scenario shows that if fishing is reduced according to previously recommended precautionary reference levels ( $F_{pa}$ ) then extinction may be postponed another 20 years (figure 3*c*), by which time the salinity drops below the absolute threshold level for cod recruitment in the Baltic Sea (Köster *et al.* 2005). Due to differences in predicted salinities between global circulation models (supplementary figure 2*b-c*), the fourth scenario includes only a minor decrease in salinity by 0.8 psu. However, the cod stock may not remain above ecologically safe levels during the coming 100 years (figure 3*d*), if exploitation is kept at  $F_{pa}$ . Hence, a strategy for adapting fishing mortalities to climate driven stock production is necessary to ensure the persistence of Baltic cod into the 22<sup>nd</sup> century.

### **(b) Adaptive management under Climate change**

The influence of both climate and fishing in determining cod stock persistence is apparent from the forecasting scenarios. Fishing reduces the age, size, and geographic diversity of populations, making them more sensitive to climate driven recruitment stress (Ottersen *et al.* 2006; Anderson *et al.* 2008). Furthermore, fish stock dynamics and persistence is influenced by “red-shifted” (i.e., positively autocorrelated) marine climate, which by amplifying stock variance may ultimately increase the risk of extinction (Steele & Henderson 1984). Since Baltic cod is close to its physiological tolerance level, such changes in amplitude and duration of extreme climate events (i.e., the frequency and duration of Baltic inflow events) are very likely to have greater consequences than changes in mean values (Brander 2007). In the first analysis, the probability of collapse increases

steeply and non-linearly with  $F$  and decreasing salinities (figure 4a). If salinity decreases by only 0.8 psu cod is likely to persist, however if the decrease is 4.8 psu a collapse seems inevitable. The previously recommended precautionary fishing mortality ( $F_{pa} = 0.6$ ) results in a ~50% risk of collapse even without changes in climate, which is clearly not an acceptable level of precaution. If implemented, the current EC management plan (EC 2007) which gradually reduces exploitation to  $F_y$  (i.e., the target exploitation level of 0.3) may allow for sustainable exploitation of the cod stock, however, only given a decline in mean salinity of <1 psu.

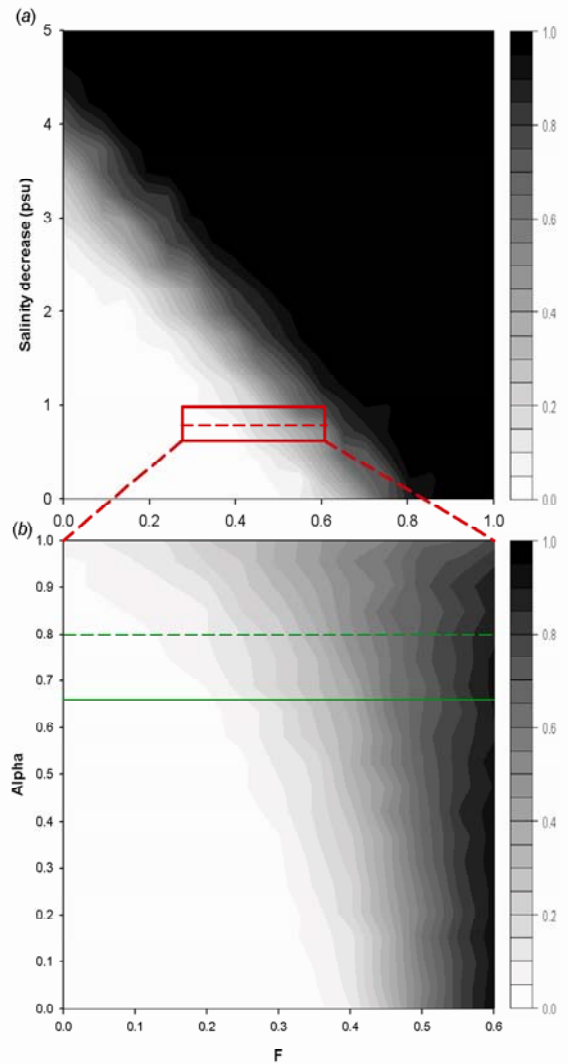


Figure 4. Probability of cod stock falling below ecologically safe levels ( $B_{lim}$ ) given future changes in climate and fishing mortalities. (a) Probabilities are calculated from simulations of mean decrease in salinity from 0-5 psu and  $F$  levels from 0 to 1. In (b) the additional effect of increasing environmental autocorrelation in future climate time-series (i.e.,  $\alpha$  from 0 to 1) is investigated by studying the change in the slope of the “probability landscape” at a projected salinity decline of 0.8 psu specifically (see red square in a). Simulations were conducted over a range of fishing mortalities ( $F$  from 0 to 0.6) while the projected increase in SST remained fixed at 3.5 °C. The green solid line mark the actual  $\alpha$  in the salinity time-series, while the dashed line aim to represent a correction for possible underestimations of forecasted GCM autocorrelations, i.e., here set to a maximum of 20%. White areas indicate low probabilities of cod biomass being below ecologically safe limits ( $B_{lim}$ ), while black areas demonstrate high probabilities.

In the second analysis, an added increase in environmental autocorrelation amplifies the probability of collapse (figure 4b) due to an elevated risk of prolonged periods of poor salinity conditions for spawning and recruitment of Baltic cod. Furthermore, the effect is

more pronounced at high levels of alpha ( $\alpha$ ) demonstrating an increasing synergy between fishing and climate effects in positively autocorrelated environments. However, given the minor underestimation of observed autocorrelations in global climate projections (Wigley *et al.* 1998) (i.e., here illustrated by a maximum deviation of 20% from the observed level of alpha) the relative increase in the risk of stock collapse is rather limited ( $< 10\%$ ). (Note however, that since population variance increase over time in “red-shifted” marine environments (Steele & Henderson 1984), the relatively short time-scale of our simulations (i.e., 100 years) may actually underestimate the long-term effects of environmental autocorrelation on stock persistence (i.e., normally simulated over 1000 years; Ripa & Lundberg 1996)). Nevertheless, it is evident that a sustainable strategy for managing exploitation must be adapted to several aspects of climate change. In our final section we provide recommendations on exploitation levels that maximize long term sustainable yield (MSY) under climate change and for an acceptable level of risk.

### **(c) *Towards sustainable development in the Baltic Sea***

In contrast to the traditional (and indeed controversial) use of MSY, which aims to maximize biological production of target stocks irrespective of climate and indirect effects of non-target species (Hilborn 2007), MSY is here defined as the theoretical equilibrium yield that can be safely harvested from a stock under different climate conditions defined by both direct effects on recruitment and indirect effects of species interactions on growth and survival of Baltic cod (i.e., through the prey species sprat and herring). We initially computed the theoretical carrying capacity (K) of Baltic cod at zero exploitation and at various salinity and SST levels resembling the projected changes in Baltic Sea climate by 2100. The reproductive volume (MaKenzie *et al.* 2000), i.e., the maximum geographic range and habitat available for successful reproduction of Baltic cod is largely determined by salinity (and oxygen) levels in the Gotland Basin, the largest and northernmost spawning area of cod in the Baltic Sea (supplementary figure 2). Our simulated K, reaching mean levels of 630 Kt under historical salinity and SST levels (figure 5a) corresponds closely to peak SSB levels during the early 1980s (670 Kt), a period referred to as “the gadoid outburst” when cod inhabited almost the entire Baltic Sea (Bagge *et al.* 1994). At K the cod population is mainly limited by intra-specific competition for the available resources, i.e., food-availability and reproductive habitat. Hence, the theoretical K reached is due to the

combined outcome of food-availability through the interactions with the prey species herring and sprat and the positive effect of salinity on the size of the reproductive habitat. Additionally, both SST and the availability of the key zooplankton prey, *Pseudocalanus acuspes* indirectly limit cod K by influencing the recruitment of the prey species. Thus, our simulations appear to capture the main external and internal mechanisms explaining climate effects on carrying capacity of Baltic cod.

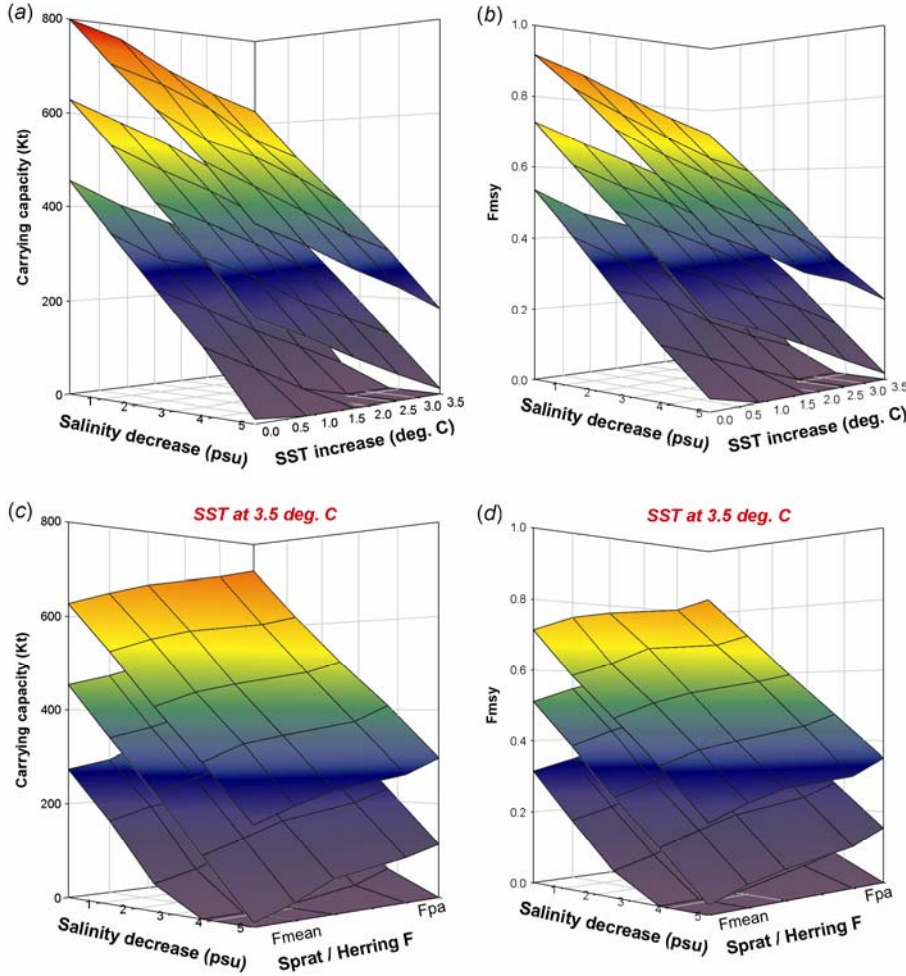


Figure 5. A sustainable management strategy for Baltic cod under different scenarios of climate change. In (a) and (b) the theoretical carrying capacity and corresponding maximum sustainable fishing mortality ( $F_{msy}$ ) for Baltic cod is shown for each combination of projected changes in salinity and SST. In order to address the indirect effects of species interactions on cod stock response to climate change, the lower panels (c, d) include fishing pressures for sprat and herring, given a projected increase in SST by 3.5°C. Fishing mortalities range from mean historical levels ( $F_{mean}$ ) to the recommended precautionary levels ( $F_{pa}$ ) for sprat and herring respectively (supplementary figure 5). The middle planes represents mean K and  $F_{msy}$  while upper and lower planes respectively illustrate the upper and lower confidence levels of each scenario.

The biomass supporting MSY ( $B_{msy}$ ) is derived as the point of maximum population growth and is located at  $K/2$ . By solving the model equation (i.e., Eq. 2) for the level of  $F$  that under given changes in salinity and SST conditions yields  $B_{msy}$ , the maximum sustainable fishing mortality ( $F_{msy}$ ) is shown decreasing with both salinity and increasing SST (figure 5b). This can be explained by a direct salinity effect on cod recruitment (i.e., through egg and larvae survival; Köster *et al.* 2005) and an indirect SST effect channeled through species interactions; due to increased recruitment of sprat and a competition driven decline in herring eventually affecting the dominance and availability of prey for cod. Hence, the degree to which species interactions may either buffer or accentuate the cod stock response to climate change depends on the nature of both positive and negative feedback loops within the food-web (Ives 1995).

In order to illustrate the need for multi-species management in mitigating climate effects on Baltic cod, we repeated the above analysis including different fishing pressures on sprat and herring as well. Thus, for each combination of salinity and fishing mortalities, i.e., ranging from mean historical levels ( $F_{mean}$ ) to the recommended precautionary levels ( $F_{pa}$ ) for sprat and herring respectively (supplementary figure 4), we estimated the theoretical  $K$  and  $F_{msy}$  for cod given a projected increase in SST by 3.5 °C (figure 5c-d). As in the previous analysis both  $K$  and  $F_{msy}$  decrease with salinity conditions, however we may partially offset the indirect SST effect on cod by adapting fishing pressures to the recruitment potential of sprat and herring respectively. Note however that accounting for these indirect SST effects through prey availability may not be sufficient to overcome any additional impacts of higher SST acting on oxygen consumption rates in the deep basins of the Baltic Sea, thus potentially reducing oxygen conditions and the size of the reproductive habitat for Baltic cod (MacKenzie *et al.* 2007).

#### 4. CONCLUSIONS

The simulations presented above are intended to provide guidance in developing sustainable management for Baltic cod and to show the risks associated with different strategies. To that end, our ecosystem-based approach provides quantitative stock forecasts and suggests appropriate management actions to mitigate negative effects on future fisheries production under climate change. Furthermore, our ecosystem-based approach is



intended to inform and thus strengthen the institutional and political will needed for successful implementation and governance of future EBFM in the Baltic Sea (Hilborn 2007). Despite the difficulties inherent in forecasting, fisheries scientists should face the challenges of providing reliable forecasts to managers and stake-holders planning for the future. Although specifically fitted to the Baltic Sea, a low-diversity ecosystem highly sensitive to climate change, the methodology presented here is flexible enough to be used for other ecosystems, drivers (environmental or anthropogenic) and uncertainties, given adequate time-series for the particular ecosystem (Ives *et al.* 2003). Adopting similar ecosystem-based approaches elsewhere will move us towards long-term sustainability in marine fisheries worldwide.

### *Acknowledgements*

We wish to thank M. Meier for support concerning climate forecasting and F. Köster for general comments and input. M.L. was funded by the EU Marie Curie EST project METAOCEANS (MEST-CT-2005-019678) and C.M. by the German Science Foundation through the Excellence Cluster "Integrated Climate System Analysis and Prediction (CliSAP) at the University of Hamburg. This study is a contribution to the European Union 6<sup>th</sup> Framework Projects "Resolving Climatic Impacts on Fish Stocks" (RECLAIM, 044133) and "Understanding the mechanisms of stock recovery" (UNCOVER, 022717).

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Table 1. Parameter estimates and ecological mechanisms underlying the effects of species interactions, fishing and climate/zooplankton on Baltic cod, sprat and herring in the BALMAR food-web model (Lindegren *et al.*, 2009).

<b>Interaction</b>	<b>Parameter</b>	<b>Ecological mechanism</b>	<b>Suggested references</b>
Cod - Cod	0.67*	Density dependence / Cannibalism	Sparholt (1994); Neuenfeldt & Köster 2000
Herring - Cod	0.23	Foraging effect on growth	Sparholt (1994); ICES (1996)
Sprat - Sprat	0.90*	Intra-specific competition / Egg cannibalism	Köster & Möllmann (2000); Mackenzie & Köster (2004)
Cod - Sprat	-0.06	Predation mortality	ICES (1996); MacKenzie & Köster (2004)
Herring - Herring	0.87*	Intra-specific (food) competition	Möllmann <i>et al.</i> (2005)
Cod - Herring	-0.09	Predation mortality	Sparholt (1994); ICES (1996)
Sprat - Herring	-0.10	Inter-specific (food) competition	Sparholt (1994); Möllmann <i>et al.</i> (2005)
Fishing - Cod	-0.91	Fishing mortality	ICES (2007)
Fishing - Sprat	-0.34	Fishing mortality	ICES (2007)
Fishing - Herring	-0.82	Fishing mortality	ICES (2007)
Salinity - Cod	0.08	Egg/larvae survival (recruitment)	Nissling (1994); Köster <i>et al.</i> (2005)
SST - Sprat	0.08	Egg/larvae survival (recruitment)	Mackenzie & Köster (2004)
Z** - Herring	0.15	Prey availability, growth/survival (recruitment)	Möllmann <i>et al.</i> (2003); Möllmann <i>et al.</i> (2005)

\* Parameters < 1 indicate an increasing degree of density dependence in the population.

\*\* *Pseudocalanus acuspes*

## Supplementary figures

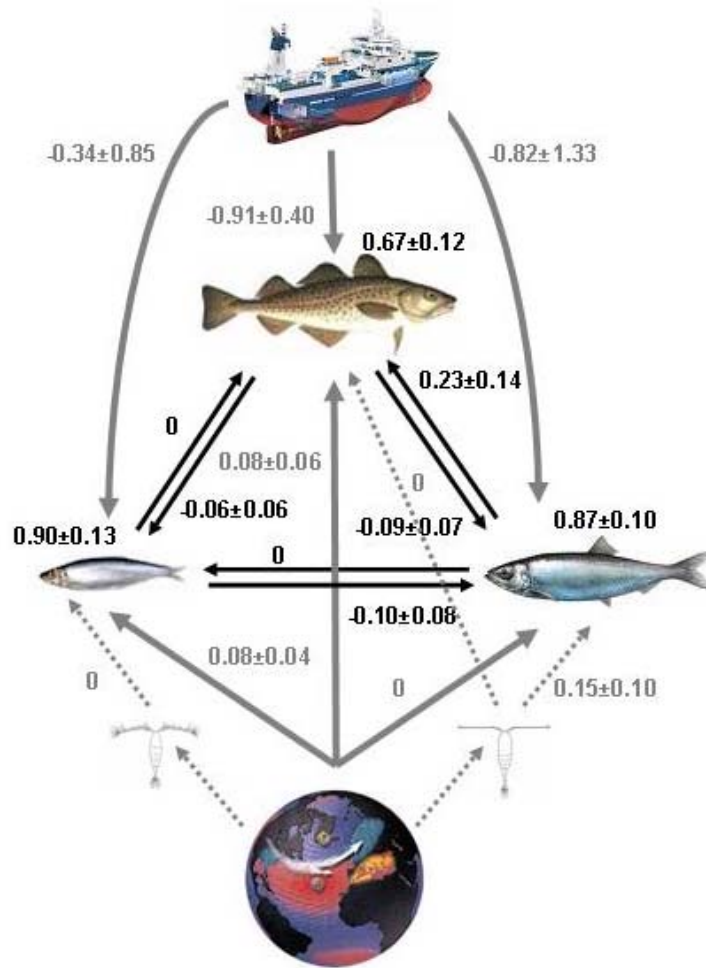


Figure 1. A schematic view of the Baltic Sea upper-trophic food web. Black arrows and parameters represent species interactions between cod (top), sprat (left) and herring (right). Grey arrows and parameters demonstrate the effects of fishing, climate and zooplankton on the three species respectively. (Interactions with the key zooplankton species *Acartia* spp. (left) and *Pseudocalanus acuspes* (right) are illustrated by dotted arrows). Negative parameter values indicate negative effects on the biomass of the species and vice versa. (Intra-specific parameters <1 indicate an increasing degree of density dependence in the population). Zero parameter values indicate interactions excluded during model selection. Note that although statistically uncertain we decided to include the fishing effect on sprat and herring since they are heavily exploited by commercial fishing. (Figure from Lindegren *et al.* 2009).

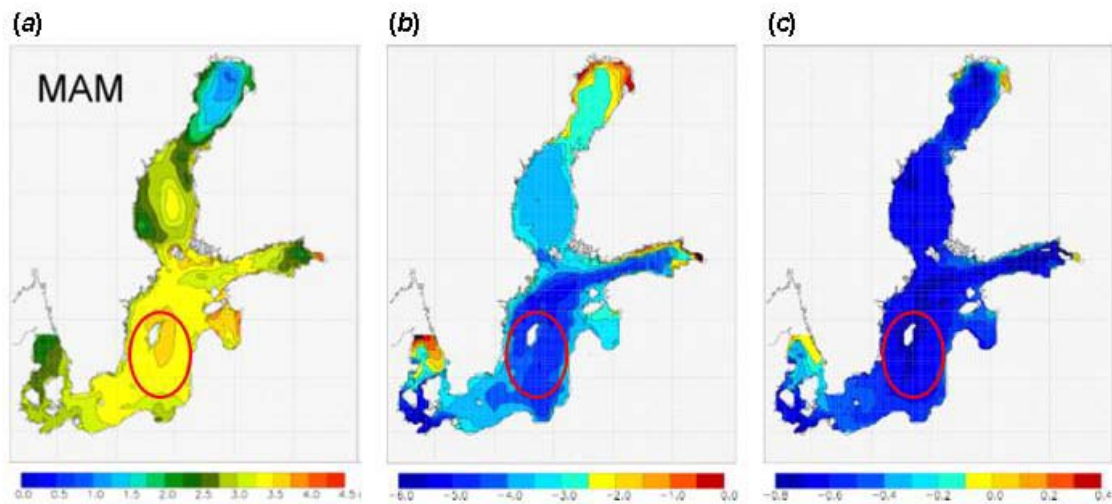


Figure 2. Projected changes in (a) spring sea surface temperature and (b, c) annual vertically averaged salinities in the Baltic Sea by 2071–2100. The red ellipse marks the projected climate changes in the Bornholm Basin, i.e. the northernmost and largest spawning basin for Baltic cod. Each panel is an ensemble average of 16 scenario simulations based upon seven RCMs, five GCMs and IPCC emission scenarios A2 and B2 conducted within the European PRUDENCE project. Salinity projections from two different models for the IPCC A2 CO<sub>2</sub> scenario are shown where (b) applies global forcing of the Rossby RCM provided by the ECHAM4/OPYC3 model and in (c) global forcing of the Rossby RCM was provided by the HadAM3H model. See Meier (2006) and Meier *et al.* (2006) for details. (Figures from Meier 2006).

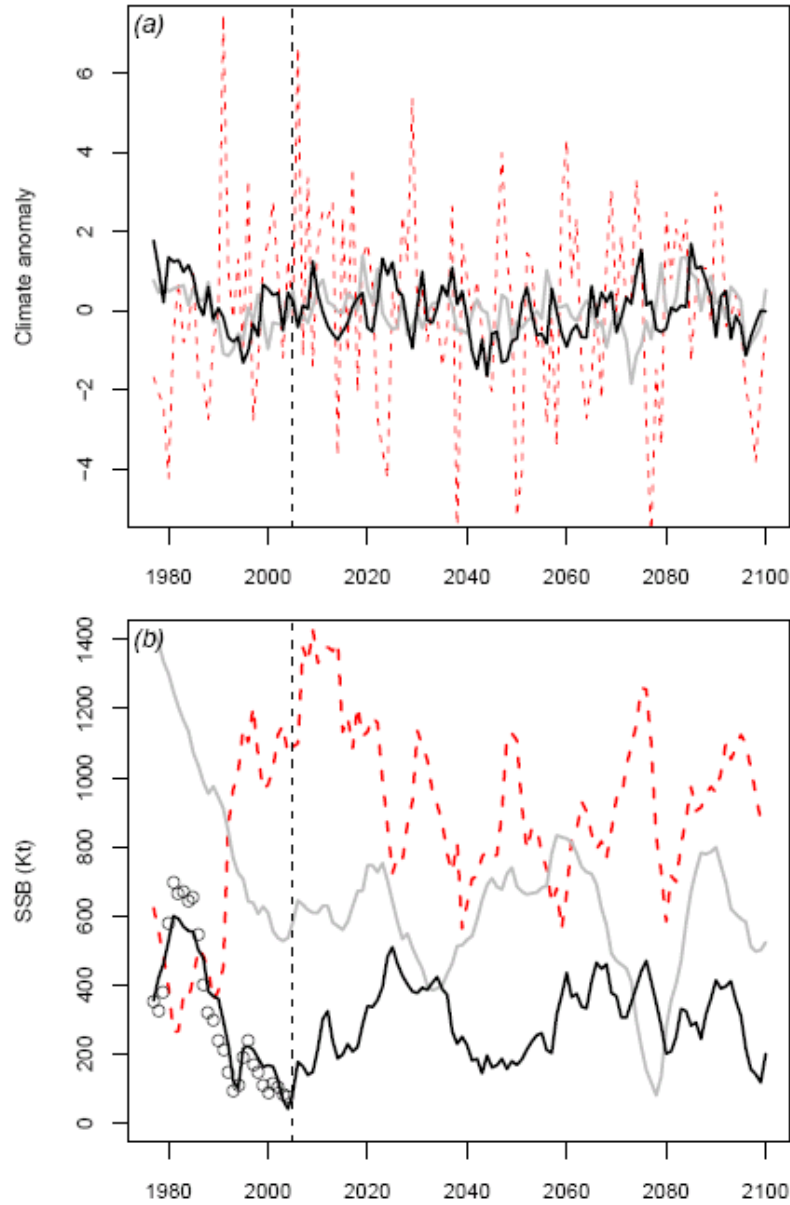


Figure 3. A single model replication from the coupled climate – food-web model. In the upper panel (a) climate simulations of past and future SST (red-dashed), salinity (black) and *Pseudocalanus* abundance (grey) are shown as anomalies (i.e. standardized to zero mean). In the lower panel (b) the response of sprat (red-dashed), cod (black) and herring (grey) spawning stock biomasses (Kt) are shown. In the above example climate and fishing mortalities remain at mean historical levels with the exception of  $F$  for cod which is set to the precautionary fishing mortality,  $F_{pa}$ . Simulations are initiated in 1977 and reproduce very well the historical dynamics of the fish stocks, e.g. compare with the observed SSB values for cod (circles).



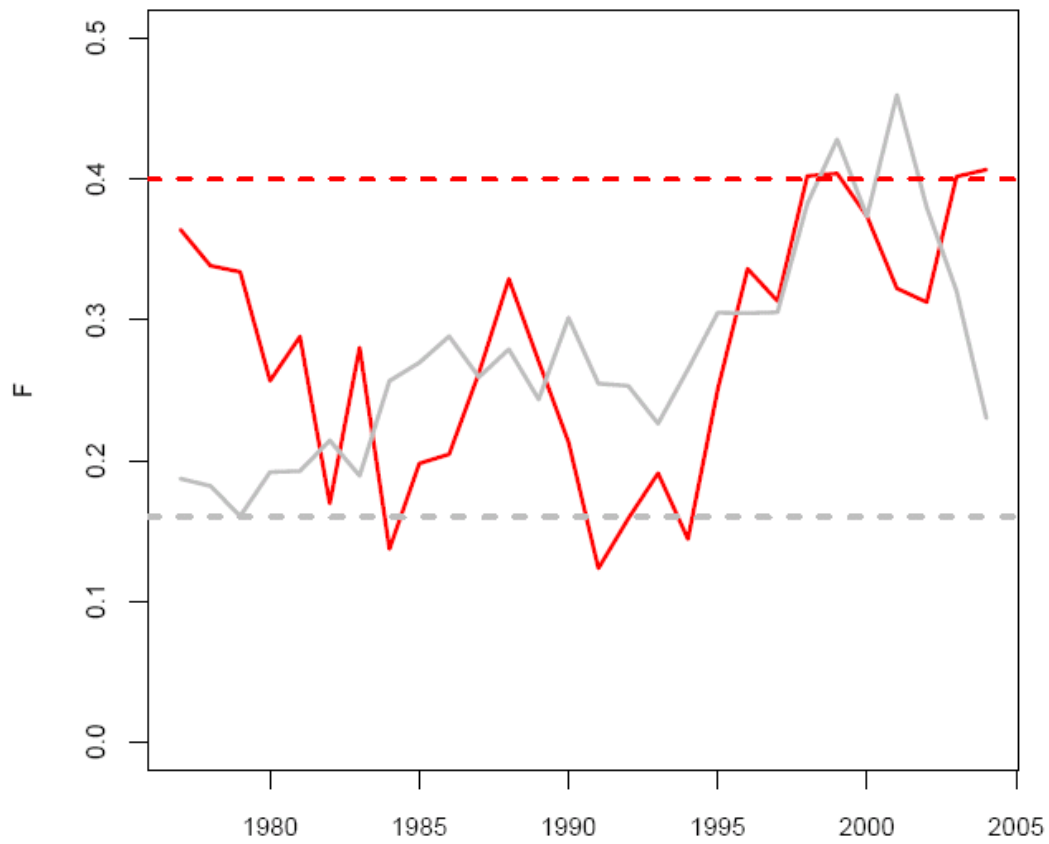


Figure 4. Historical fishing mortalities for Baltic sprat (red) and herring (grey) from 1977-2004. Horizontal dashed lines mark the recommended precautionary fishing mortalities ( $F_{pa}$ ) for sprat (red) and herring (grey) respectively.





## ***Biomanipulation - a tool in Marine Ecosystem Management and Restoration?***

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### ***Abstract***

Widespread losses of production and conservation values make large-scale ecosystem restoration increasingly urgent. Ecological restoration by means of biomanipulation, i.e., by fishing out planktivores as to reduce the predation pressure on herbivorous zooplankton, has proven an effective tool in restoring degraded lakes and coastal ecosystems. Whether biomanipulation may prove a useful restoration method in open and structurally complex marine ecosystems is however still unknown. To promote a recovery of the collapsed stock of Eastern Baltic cod (*Gadus morhua*), large-scale biomanipulation of sprat (*Sprattus sprattus*), the main planktivore in the Baltic Sea, has been suggested as a possible management approach. We study the effect of biomanipulation on sprat using a statistical food-web model which integrates internal interactions between the main fish species of the Central Baltic Sea with external forcing through commercial fishing, zooplankton and climate. By running multiple, stochastic simulations of reductions in sprat spawning stock biomass (SSB) only minor increases in cod SSB were detected, none of which brought the cod significantly above ecologically safe levels. On the contrary, reductions in cod fishing mortality and/or improved climatic conditions would promote a significant recovery of the stock. By this we demonstrate that an ecosystem-scale biomanipulation with the main focus of reinstating the dominance of cod in the Baltic Sea may likely be ecologically ineffective, operationally difficult and costly. We argue that reducing exploitation pressure on Eastern Baltic cod to ecologically sound levels is a far more appealing management strategy in promoting a long-term recovery and a sustainable fishery of the stock.

## 1. Introduction

Widespread losses of production and conservation values make large-scale ecosystem restoration increasingly urgent (Hobbs and Norton 1996). As ecosystems may exist in alternative stable states i.e., dynamic regimes (Scheffer et al. 2001, Scheffer and Carpenter 2003), adopting a dynamic concept for ecosystem management and restoration is essentially needed (Mayer and Rietkerk 2004). Ecological restoration is the process of enhancing ecosystem recovery by means of artificial manipulations (Dobson et al. 1997) and involves pushing an ecosystem back to a desired regime (i.e., with particular structural and functional characteristics; Palik et al. 2000) while minimizing ecological risks, such as species invasions (Mack et al. 2000). Rooted firmly in ecological theory (Hairston et al. 1960, Palmer et al. 1997), manipulations have proven efficient in restoring degraded terrestrial ecosystems (Shachak et al. 1998, Barrett-Lennard 2000, Gomez-Aparicio et al. 2004, Cummings et al. 2005) as well as dysfunctional lakes and coastal ecosystems (Shapiro and Wright 1984, Carpenter et al. 1987, Paine et al. 1985, Bergman et al. 1999b, Hawkins et al. 1999). Due to difficulties in controlling ecological processes on vast spatial scales (e.g., drift and migrations), restorations of open marine ecosystem have so far been absent.

In the early 1990s, the Central Baltic ecosystem shifted rapidly from a cod (*Gadus morhua*) dominated to a sprat (*Sprattus sprattus*) dominated ecosystem state (Köster et al. 2003, Möllmann et al. 2008). This regime shift was likely triggered by coinciding overfishing and climate change, causing high cod egg and larval mortalities and eventually recruitment failure due to low salinity and hypoxia (Köster et al. 2005, Möllmann et al. 2008). Following the collapse of the cod stock, sprat was released from predation (Köster et al. 2003, Möllmann et al. 2008). In combination with temperature driven recruitment success (MacKenzie and Köster 2004) the stock rose to unprecedented levels. The large sprat stock may now impose key negative feedbacks by preying on cod eggs (Köster & Möllmann 2000) and reducing the main food of cod larvae (i.e., the copepod *Pseudocalanus acuspes*) (Möllmann & Köster 2002), thus maintaining the ecosystem in its currently less desirable ecosystem state (Bakun & Weeks 2006, Möllmann et al. 2008).

Biomanipulation has often proven an effective management tool in reinstating top-predator regulation in shallow lakes (Shapiro et al. 1975, Hansson et al. 1998, Drenner & Hambright 1999, Bergman et al. 1999b). Traditionally, biomanipulation means managing the fish community by selectively fishing out planktivores and/or restocking predators as to reduce the predation pressure

on herbivorous zooplankton. An increased abundance and size of zooplankton theoretically leads to higher grazing pressure on phytoplankton and further to improved water quality (Hansson et al. 1998). Despite the development of ecosystem-based approaches to fisheries management (EBFM), i.e., integrating multiple internal and external drivers (e.g., species interactions, fishing and climate) in a common framework (Pikitch et al. 2004, Marasco et al. 2007), biomanipulation has never been used in marine management and restoration. However, to promote a recovery of the collapsed stock of Eastern Baltic cod large-scale biomanipulation has been suggested a possible management approach for the Baltic Sea (Carlgren 2007). By selective fishing on sprat, this approach aims to weaken the negative feedbacks on cod recruitment and to reinstate top-predator regulation in the open and coastal areas of the Baltic Sea (Fiskeriverket 2008). Whether biomanipulation may prove a useful restoration method in heterogeneous and structurally complex large marine ecosystems is however still unknown.

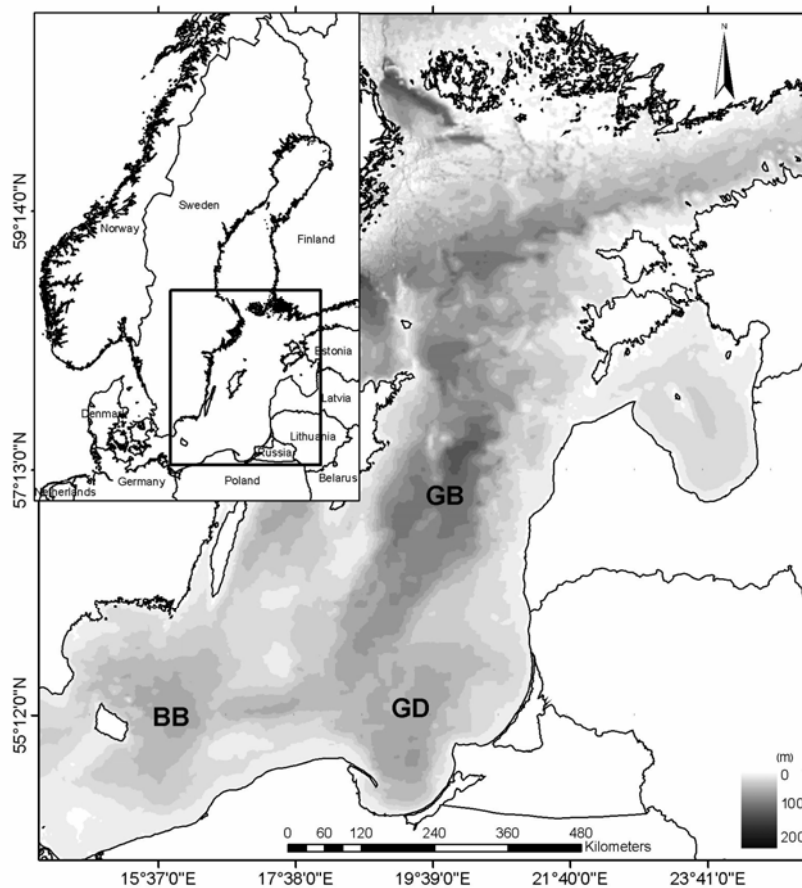
Here we study the feasibility of a large-scale biomanipulation of sprat in promoting the recovery of Eastern Baltic cod using a statistical food-web model integrating internal species interactions between the major Baltic fish populations cod, sprat and herring (*Clupea harengus*) with external forcing through commercial fishing, zooplankton and climate (Lindegren et al. 2009). Our simulations show that basin-scale biomanipulation of sprat is a largely ineffective, operationally difficult and costly management option in promoting a recovery of Eastern Baltic cod.

## **2. Material and Methods**

### *2.1 Ecosystem and site description*

The Baltic Sea is a large semi-enclosed sea separated from the North Sea by a number of narrow straits and shallow sills (Fig. 1). Due to its brackish conditions (i.e., vertically averaged salinity of ~8 psu) the Baltic Sea ecosystem is characterized by low species diversity, but high productivity. The central part of the Baltic Sea encompasses three deep basins, i.e., the Bornholm Basin, the Gdansk Deep and the Gotland Basin (Fig. 1). Characteristic to the hydrography of these basins is a permanent halocline separating low salinity surface waters from high saline deep waters (i.e., at ~70-100 meters). Deepwater conditions can only be enhanced by inflows of saline and oxygenated water from the North Sea (Matthäus and Franck 1992). A lack or low frequency of these events, as observed during the recent three decades, leads to low salinity and oxygen levels and hence detrimental reproductive conditions for e.g., cod (Köster et al. 2005). Climatic conditions since the

late 1980s have significantly changed the living conditions for animal populations inhabiting the area. The main trends are lowered salinity and oxygen levels due to low inflow frequency and increased temperatures (Möllmann et al. 2009). Additionally the Baltic Sea is presently in a eutrophied state as compared to the 1950s and before (Österblom et al. 2007).



**Figure 1.** Map of the Baltic Sea and its location within Northern Europe. The central part of the Baltic Sea encompasses three deep basins, i.e., the Bornholm Basin (BB), the Gdansk Deep (GD) and the Gotland Basin (GB).

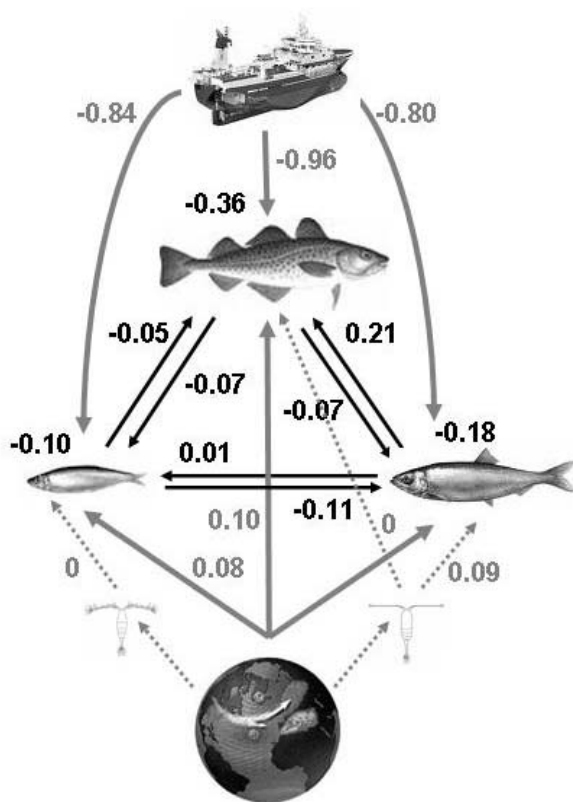
## 2.2 The food-web model

We studied the dynamics of Baltic cod, sprat and herring under a number of biomanipulation scenarios using the BALMAR food-web model (Lindegren et al. 2009), a linear state-space model based on a theoretical approach for modeling long-term population dynamics (Ives et al. 2003). The approach, a first-order multivariate autoregressive model (MAR(1)) applies a statistical framework for modeling species interactions at multiple trophic levels (Ives et al. 2003) and essentially functions as a set of lagged multiple linear regression equations (one for each species of the food web) solved simultaneously to arrive at the most parsimonious model overall (Hampton and Schindler 2006). Written in state-space form, the MAR(1) model we used is given by:

$$\mathbf{X}(t) = \mathbf{B}\mathbf{X}(t-1) + \mathbf{C}\mathbf{U}(t-y) + \mathbf{E}(t) \quad (1)$$

$$\mathbf{Y}(t) = \mathbf{Z}\mathbf{X}(t) + \mathbf{V}(t) \quad (2)$$

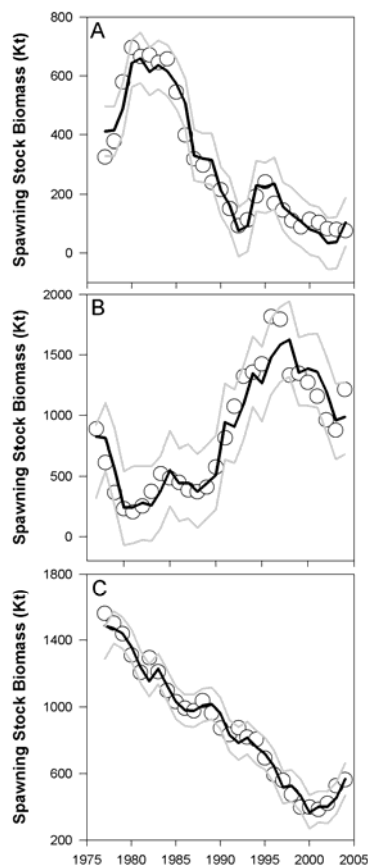
where  $\mathbf{X}$  are SSB values of cod, sprat and herring derived from multi-species fish stock assessment for the Baltic Sea (ICES 1996) at time  $t$  and  $t-1$  respectively, and  $\mathbf{B}$  is a 3 x 3 matrix of species interactions, an analogue of the “community matrix” used by May (1972) and Pimm (1982). Encompassing the effects of commercial fishing and climate-driven ecosystem dynamics, the covariate vector  $\mathbf{U}$  contains values of mean annual fishing mortalities ( $F$ ) and a number of selected climate variables known to affect recruitment of cod, sprat and herring respectively. Consequently,  $\mathbf{C}$  is a 3 x 9 matrix whose diagonal elements specify the effect of covariates on each species. The process error  $\mathbf{E}(t)$  is assumed multivariate normal and temporally uncorrelated. Likewise, the observation error of the covariance matrix of the normal random variable  $\mathbf{V}(t)$  is assumed independent. Regression parameters were found by maximum likelihood estimation using a Kalman filter (Harvey 1989). The Kalman filter is a recursive estimator that sequentially calculates the unobserved values  $\mathbf{X}(t)$  from the previous time step ( $t-1$ ) using the model formula specified in Eq. 1. Predictions from the “hidden” state are then updated using the observed values,  $\mathbf{Y}(t)$  of the “true” state (Eq. 2). Model fitting was performed on available time series covering the period 1974-2004.



**Figure 2.** A schematic view of the Central Baltic Sea upper trophic food web. Black arrows and parameters represent interactions between cod (top), sprat (left) and herring (right), i.e., density dependence, competition and predation. Grey arrows and parameters demonstrate top-down effects of fishing and bottom-up effects of climate and zooplankton on the dynamics of the three species respectively. (Interactions with the key species *Acartia* spp.(left) and *Pseudocalanus acuspes* (right) are illustrated by dotted arrows). Negative parameter values indicate negative effects on the biomass of the species and vice versa. Parameters with zero values do not significantly aid in explaining the variation in SSB and were thus excluded during model reduction.



The fitted model captured accurately the known mechanisms of species interactions within the Baltic Sea food-web, i.e., density-dependence (Neuenfeldt and Köster 2000, Köster and Möllmann 2000a), competition (Möllmann et al. 2005) and predation (Sparholt 1994), (i.e., as demonstrated by the negative signs of species interaction coefficients in Fig. 2). Furthermore, the model parameters also illustrate the negative effect of fishing and the positive effect of zooplankton and climate on recruitment of cod (Köster et al. 2005), sprat (MacKenzie and Köster 2004) and herring (Möllmann et al. 2005) respectively (Fig. 2). The fitted model reproduces well the historical fish stock dynamics in the Baltic Sea (Fig. 3). These are characterized by the collapse of the cod stock from high levels during the early 1980s, the drastic increase of the sprat stock since the late 1980s, and a constant decline of herring biomass. Being able to accurately “recreate the past”, the response of the fish community to a number of future biomanipulation scenarios was studied.



**Figure 3.** Historical development of the Baltic Sea fish populations. The fitted biomass values (black) represent well the observed biomasses (circles) of (A) cod ( $r^2=0.95$ ), (B) sprat ( $r^2=0.89$ ) and (C) herring ( $r^2=0.98$ ) from 1977-2004. Upper and lower 95% prediction intervals are displayed by grey lines.

### 2.3 Model simulations

#### 2.3.1 Ecological scenarios

Hansson et al. (1998) give several recommendations for conducting a successful biomanipulation: (i) the reduction in planktivore biomass should be at least 75%; (ii) the reduction should be performed efficiently and rapidly within 1–3 years and (iii) efforts should be undertaken to reduce recruitment of Young-of-the-Year (YOY) fish following biomanipulation. Based on these recommendations we simulated three set of scenarios (a-c), where the first scenario (a) act as a “control scenario” with sprat F kept at the mean 1995-2004 level.

In the second set of scenarios (b1-b3), we applied a biomanipulation strategy where sprat SSB was reduced by 25, 50 and 75% respectively within three years. In order to limit recruitment of YOY sprat the stock was maintained at these reduced levels even during a follow-up period of five years. Scenarios (c1-c3) provide a management alternative to biomanipulation, where instead cod F is

reduced by 25, 50 and 75% compared to mean historical exploitation levels (1974-2004). In order to study the synergistic effects of fishing and climate we conducted each management scenarios (a-c) under two different climatic regimes, resembling alternating periods of stagnation and inflows from the North Sea respectively (Matthäus and Franck 1992). These inflow events largely determine the hydrographic conditions suitable for cod recruitment (i.e., through direct and indirect effects on egg and larvae survival) by enhancing salinity and oxygen conditions in the deep spawning basins of the Baltic Sea (Köster et al. 2005). To that end, we simulated a five-year stagnation and inflow period respectively, by decreasing/increasing salinities to minimum/maximum observed levels. During the following years of simulations we let salinities gradually approach mean historical levels again.

Scenarios were run for three years from 2005-2007 succeeded by a follow-up period of five years (2008-2012) aiming to study the long-term performance of the manipulations. All scenarios were replicated 1000 times with random process noise added at each time step. F levels (other than sprat) were set fluctuating at mean 1995-2004 levels. The degree to which the scenarios (a-c) meet the ecological objective of cod stock recovery was measured as the proportion of simulations where cod SSB increase above ecologically safe levels, i.e., the precautionary biomass level,  $B_{pa}$  (ICES 1998), either after three-years or after the five-year follow-up period. Furthermore, in order to compare the relative effects of sprat biomanipulation and reductions in cod F on the short term recovery of cod, we performed multiple stochastic simulations on combinations of sprat and cod F (ranging from 0-1.5), keeping climate conditions fluctuating at mean 1995-2004 levels. The probability of cod recovery was calculated as the percentage of simulation where cod SSB >  $B_{pa}$  (240 Kt) by 2008. All statistical analysis were conducted using the R software ([www.r-project.org](http://www.r-project.org)).

### *2.3.2 Operational scenarios*

In addition to the ecological modeling scenarios, we assessed the feasibility of conducting a large-scale biomanipulation by calculating the fishing effort needed to reduce sprat SSB by 75% over a three year period (i.e., scenario b3). Based on performance statistics (i.e., landings/kW, landings/number of vessels and landings/crew) of the pelagic fishing fleets of the Baltic Sea in 2005 (STECF, 2007) we calculated the increase in number of vessels, kW and crew needed to meet the increase in sprat landings under biomanipulation scenario (b3). In order to demonstrate the need for integrating efforts among Baltic countries, an estimation of effort increase was calculated both for

the total pelagic fleet including segments from Denmark, Estonia, Finland, Latvia, Lithuania, Poland and Sweden as well as for the Swedish fleet segment separately.

### 2.3.3 Economic scenarios

Secondly, we performed a brief bio-economic analysis aiming to quantify economic value of future landings from management scenarios (b) and (c), respectively. Net present value (NPV) is a standard method for measuring the financial appraisal of long-term projects and is widely used in fisheries economics (Sumaila 2004, Döring and Egelkraut 2008). In calculating NPVs, normally the net cash flow expressed as the difference between income and costs is used. However, since no reliable estimates of fishing cost are available for Baltic sprat and herring (for cod see: Eggert and Tveterås 2007, Döring and Egelkraut 2008, Röckmann et al. 2008) we calculated the NPV of future landings without subtracting fishing costs for scenario (b) and (c) respectively as given by the formula:

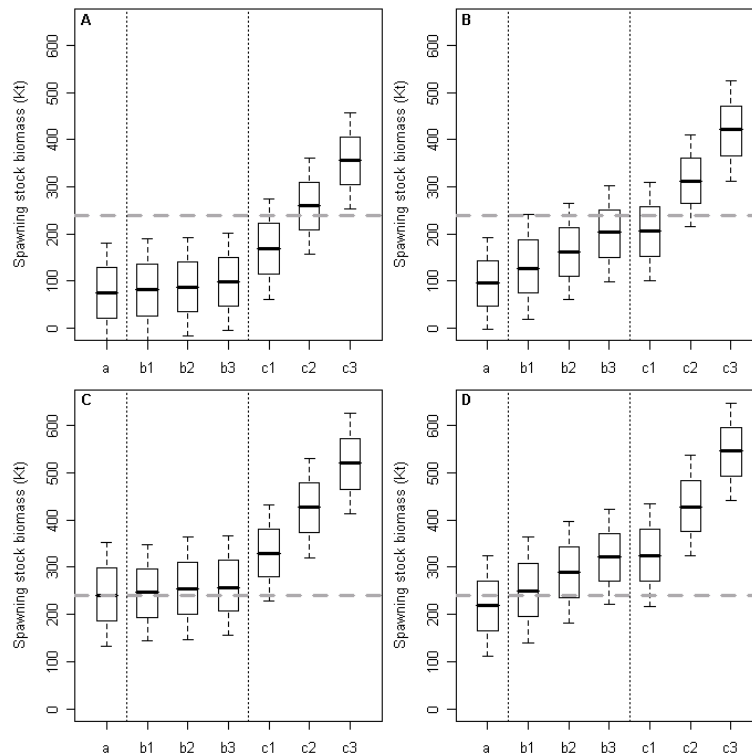
$$NPV_{(b, c)} = \left( \sum_{t=1}^8 e^{-\delta t} \{p_i[L_i(t)]\} * L_i(t) \right) - NPV_{(a)}, \quad (3)$$

where for all years  $t$  (2005-2012), the NPV is the sum of market price  $p_i$  (m€/Kt) multiplied with landings  $L_i$  (Kt) for all species  $i$  of the fishery (i.e., cod, sprat and herring). Finally, the  $NPV_{(a)}$  of the control scenario (a) was subtracted to yield the net economic value of landings from management scenarios (b) and (c) respectively. To account for financial risks we applied a discount rate ( $\delta$ ) of 25%. Large discount rates (often ranging from 25-40%) are typical in fisheries and are mainly due to the great uncertainty perceived about future landings (Hillis and Wheelan, 1994). Further we considered two versions of Eq. 3, where in the first we applied a constant market price for all years, while in the second we let market price depend on supply, i.e., the price decrease with landings. Parameters were calculated from the observed market prices (adjusted for inflation by multiplying with the inflation rate for each year) and landings from 1984-2004.

### 2.3.4 Management strategy evaluation

In order to select the most appropriate management strategy in promoting a recovery of Eastern Baltic cod, we summed up by performing a brief Management Strategy Evaluation (MSE). MSE involves assessing the consequences of a range of management options and laying bare the trade-offs in performance across a range of management objectives (Smith et al. 1999). In this study we defined three main objectives: (i) an ecological objective of promoting a recovery of cod above

ecologically safe levels, (ii) an operational objective of finding a feasible fishing effort in implementing the management option and finally (iii) an economic objective of maximizing the cost effectiveness of the management option chosen. The performance of each scenarios (a), (b) and (c) was ranked in terms of their fulfillment of these management objectives by assigning a score from 1 to 5 (i.e., with 5 corresponding to a complete fulfillment of the management objective).



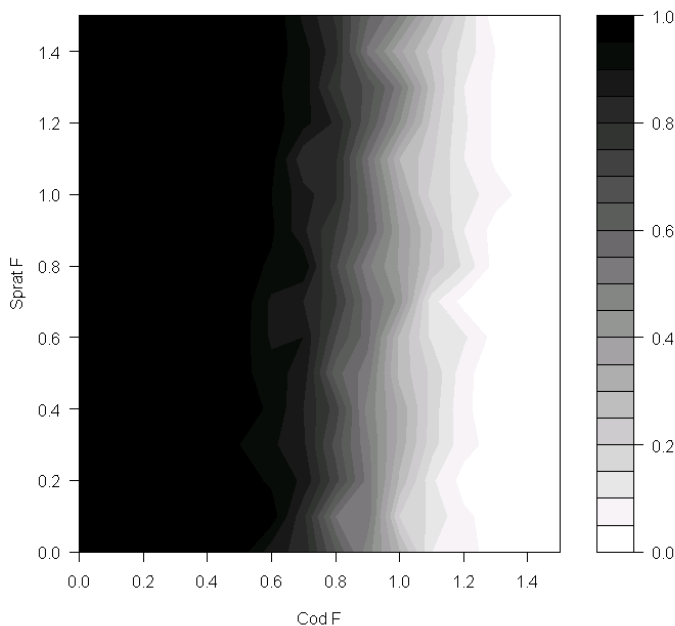
**Figure 4.** Simulated SSB of Baltic cod under management scenarios (a-c), where scenario (a) refers to status-quo conditions, scenarios (b1-b3) to a 25, 50 and 75% reduction in sprat SSB (i.e., biomanipulation) and scenarios (c1-3) to a 25, 50 and 75% reduction in cod F. The short- (left) and long-term response (right) of the cod stock are shown for two climate regimes, resembling alternating periods of unfavorable (A, B) and favorable (C, D) hydrographic conditions for spawning and recruitment of Eastern Baltic cod. The horizontal dashed line represents the precautionary stock size ( $B_{pa}$ ) above which the cod stock is considered as recovered to ecologically safe levels. Upper and lower confidence intervals are shown for each scenario.

### 3. Results

#### 3.1 Ecological effects

During unfavorable climate conditions (i.e., low salinities due to a simulated stagnation period) the first “control scenario” (a) shows cod SSB significantly below ecologically safe levels ( $B_{pa}$ ) (Fig. 4A, B). Given reductions in sprat biomass (b1-b3), cod SSB increase slightly but still remain significantly below  $B_{pa}$  (Fig. 4A). Though a stronger long-term increase is shown after the five-year

follow-up period (Fig. 4B), a reduction in sprat SSB by up to 75% is not enough to promote a significant recovery of cod above ecologically safe levels. On the contrary, a reduction in cod F (c1-c3) demonstrates a rapid increase and gradual recovery above  $B_{pa}$ , however, significantly only for a 75% reduction in exploitation pressure. During highly favorable climate conditions (i.e., high salinities following a simulated inflow event from the North Sea) mean SSB levels of the “control scenario” (a) reach slightly above  $B_{pa}$  (Fig. 4C), only to decrease again following a gradual return to mean salinity levels during the five-year follow-up period (Fig. 4D). In response to biomanipulation (b1-b3) this decline may be counteracted and act to maintain the cod stock at or slightly above ecologically safe levels (Fig. 4D). Note however, that despite a mean increase above  $B_{pa}$  the cod stock still face a slight risk of decline below  $B_{pa}$  due to stochastic processes (e.g., as demonstrated by the sample minimum for scenario b3). As in the stagnation simulation, a reduction in cod F promotes a rapid increase in cod SSB where given favorable conditions a 50% decrease (i.e., scenario c2) is enough to promote a recovery significantly above  $B_{pa}$ .



**Figure 5.** The probability of cod stock recovery above ecologically safe levels ( $B_{pa}$ ) following sprat biomanipulation and reductions in cod F. Probabilities are calculated as the proportion of simulations where cod SSB >  $B_{pa}$  after ending biomanipulation in 2008.

In our second analysis, aiming to compare the effects of sprat biomanipulation and reductions in cod F on the recovery of cod, the probability of recovery above  $B_{pa}$  increases steeply and non-linearly with decreasing cod F but seems rather unaffected by changes in sprat F (Fig. 5). Cod F below 0.5 shows a large chance (>80 %) of recovery while F levels above 1.0 demonstrate a close to zero chance of recovery. It is worth noting that the average exploitation pressure has been very high (i.e.,  $F=0.91$ ) and has since 1997 increased well above 1.0, e.g., peaking at a staggering 1.38 in 2004.

**Table 1.** (A) Performance and capacity of the Swedish pelagic fleet as well as the total Baltic Sea pelagic fishing fleet in 2005 (STECF, 2007). (B) The mean annual increase in effort needed for successful biomanipulation in 2005 to 2007. The increase is calculated relative to the current observed capacity of the Baltic pelagic fleets in 2005 (see A). Landings (Kt) reflect the average annual increase in sprat landed. The increase in effort is calculated as the percentage increase (%) relative to current effort.

**A. Current capacity and effort (2005)**

	Vessels	kW (1000)	Crew	Landings(Kt)	L/kW(1000)	L/Vessels	L/Crew
Sweden	61	66	362	212	3.21	3.48	0.59
Total	468	163.6	2107	558.3	3.41	1.19	0.26

**B. Annual increase in landings and capacity/effort needed for biomanipulation in 2005-2007.**

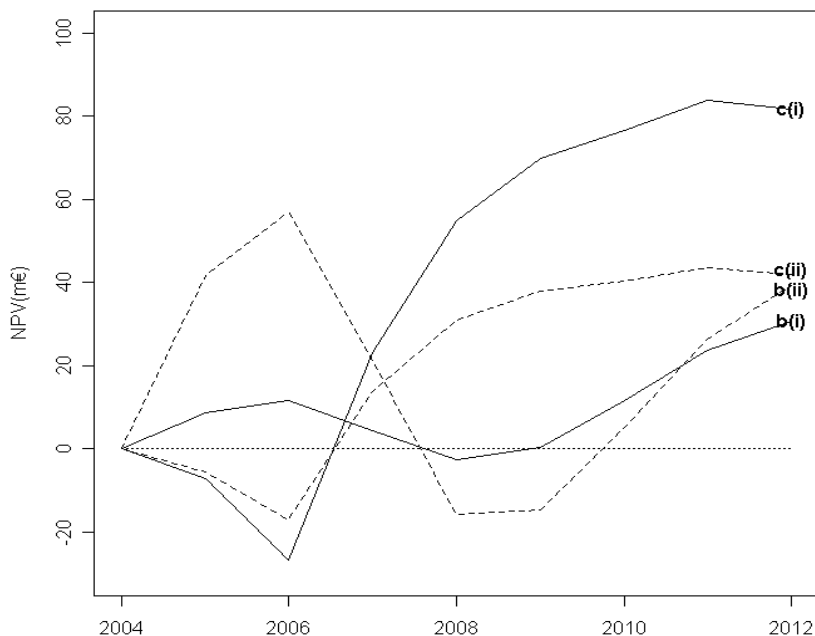
	Landings (Kt)	Effort (%)	kW (1000)	Vessels	Crew
Sweden	308	145	97	89	526
Total	308	59	96	276	1244

### 3.2 Operational effects

To evaluate the operational effects of the biomanipulation we compared the performance and capacity of the Swedish pelagic fleet as well as the total Baltic Sea pelagic fleet in 2005 (STECF, 2007) with the estimated capacity needed to perform a 75% reduction in sprat SSB over three years (Table 1). The Swedish fleet consists of 66 vessels accounting for only 13% of the total number of vessels. However, in fishing power and capacity Swedish vessels comprise some 40% of total kW. Despite the high fishing capacity, a mean annual increase in effort by 145% is needed to land an additional 308Kt of sprat in 2005, 2006 and 2007 respectively, under biomanipulation scenario (b3). This would imply an additional 89 large and modern vessels carrying an extra 526 crew members operating in the Baltic Sea. Note that since the pelagic fleet capacity is already fully exploited, i.e., spending on average 201 fishing days per year and vessel (average 1999-2004; STECF 2005), the necessary increase in effort can't be compensated for by simply increasing the number of fishing days at sea. (To fully compensate for the increase in effort, an average Swedish vessel would need to spend 493 days of the year fishing; a clearly not feasible option). If a biomanipulation management strategy would be agreed upon by all Baltic countries, a mean annual increase in effort by 59% would be satisfactory. However, this would still imply an additional 276 vessels and 1244 crew members recruited from within or outside the Baltic Sea.

### 3.3 Economic effects

The net economic value of future landings shows positive NPVs considerably above the control scenario (a) for both scenarios (b3) and (c3), i.e., the 75% reduction scenarios showing the largest increase in cod SSB (Fig. 4). When comparing NPVs of scenarios (b3) and (c3), scenario (c3) demonstrates higher NPVs amounting to 356 m€ and 186 m€ respectively, dependent on the price function used. Applying a constant mean market price yields higher NPVs than using prices as a function of supply, i.e., landings. When plotted over time, the NPV per year shows an initial decrease in scenario (c3) due to the decrease in cod landings (Fig. 6). However, as the cod stock recovers landings are allowed to increase with a net annual benefit approaching 40-80 m€ in 2012. In biomanipulation scenario (b3) the rapid increase in sprat landings yields a substantial short-term increase in NPV, followed by a drastic decrease below reference level (a) as the sprat stock approaches a minimum stock size in 2008. Coinciding with the slow increase in cod SSB, NPVs then rise gradually above reference levels. The average gross primary value per year (GPV/year) (i.e., the average value of landings per year from scenario (b3) and (c3) without subtracting the value of landings from the control scenario (a)) amounts to about 200 m€/ year and thus corresponds closely to observed values of total landing in 2003 (174 m€) and 2004 (204 m€) (STECF 2004, 2005). Hence, we feel confident in presenting likely scenarios for the effect of management on total economic value of future landings for the Baltic Sea fishery.



**Figure 6.** Annual NPVs per year for scenario (b3) and (c3) from 2004-2012. The NPVs are calculated as the net economic value (m€) of the scenario with reference to the status-quo, “control” scenario (a), shown as a dotted line. b(i) and c(i) refer to the NPVs based on a fixed market price of cod, sprat and herring while b(ii) and c(ii) show NPVs calculated on market price as a function of supply, i.e., landings.

### 3.4 Management strategy evaluation

In our brief MSE only the management scenario of reducing cod F by 75% (c3) fulfill the ecological objective of promoting a significant recovery of cod above ecologically safe levels,  $B_{pa}$ . As it may accomplish a recovery regardless of climate conditions it is assigned a performance score of 5, while the control scenario (a) and the sprat biomanipulation scenario (b3) receive scores of 1 and 3, due to the absolute lack and slight recovery of cod only during highly favorable climate conditions respectively (Table 2). Concerning the operational objective, the 100% feasibility of maintaining status-quo fishing renders a score of 5 to scenario (a) while scenario (b3) is assigned 2 due to the enormous increase in fishing effort necessary to implement biomanipulation. (If we take into account also the difficulties of performing biomanipulation without controlling sprat migration (Aro 1989), the feasibility must be considered even lower). By assigning a score of 3 to scenario (c3), we aim to reflect the trade-off between a technically simple operation of regulating cod fishing effort but a serious political difficulty in actually deciding on reduced quota. Regarding the economic objective of maximizing cost effectiveness, the status-quo scenario (a) receives the score 1 as most of the Baltic Sea fleet segments (except some pelagic fleets and coastal gill-netters) show weak or even very weak short and medium term economic performances (STECF, 2005). The poor state of the Baltic Sea fishery is indeed illustrated by a net deficit of -16 m€ in 2004. Since both scenarios (b3) and (c3) yield positive NPVs, i.e., future values of landings considerably above control scenario (a), we render them scores of 4 and 5 respectively, with 5 assigned to scenario (c3) due to its higher economic value. By summing the scores for each management scenario, with equal weightings for each objective, scenario (c3) receives the highest ranking and thus seems the most appropriate management strategy.

**Table 2.** A brief Management Strategy Evaluation (MSE) of management alternatives for the Baltic Sea. Scenarios include: the status-quo control scenario (a); biomanipulation scenario (b3) and cod fishing scenario (c3). The degree to which the scenarios fulfill the management objectives are ranked from 1-5 and finally summed to yield the most appropriate management action.

Scenarios	Management objectives			Sum of Scores
	Ecological	Operational	Economic	
a	1	5	1	7
b	3	2	4	9
c	5	3	5	13



#### 4. Discussion

In the early 1990s the Eastern Baltic cod stock collapsed due to a combination of overfishing and climate driven recruitment failure (Köster et al. 2005). The collapse of the main predator left an ecosystem almost entirely dominated by its prey, the planktivores sprat and herring now controlling zooplankton (Casini et al. 2008, Möllmann et al. 2008). This trophic cascade together with a climate-induced ecosystem regime shift potentially induced feedback-loops, keeping the ecosystem in a difficult to reverse alternative stable state (Möllmann et al. 2009). Biomanipulation, by weakening these feedback-loops, has proven an effective management tool in reinstating top-predator regulation in shallow lakes (Shapiro et al. 1975, Hansson et al. 1998, Drenner & Hambright 1999, Bergman et al. 1999b). In this study, we have simulated a number of management scenarios including large-scale biomanipulation of sprat and evaluated their ecological, operational and economic effects on meeting the primary management objective of promoting a recovery of Eastern Baltic cod.

Our model simulations revealed that the artificial reduction in sprat biomass would be largely ineffective in restoring the Eastern Baltic cod stock. We argue that this is due to the lower importance of the two suggested feedback mechanisms, i.e., egg and *P. acuspes* predation relative to the effect of hydrography on cod recruitment success. Earlier studies have demonstrated the detrimental effect of low salinity and oxygen on cod egg survival (reviewed in Köster et al. 2005). When fitting an environmentally-sensitive cod stock-recruitment relationship with averaged salinity of the deepest basin of the Central Baltic Sea as only environmental factor, Heikenheimo (2008) managed to explain 85% of the variation in cod recruitment from 1974-2004. Thus, Heikenheimo (2008) support the notion that hydrographic conditions play the by far dominating role in regulating recruitment success of Baltic cod. In our statistical food-web model we do however, find a slight negative feedback of sprat on cod. Nevertheless, when compared to the large external effects of commercial fishing and changing salinity conditions on the dynamics of cod SSB, its impact must be considered relatively small. The reason behind this limited effect may be that also the feedback mechanisms are critically dependent on the hydrographic situation and hence are reflected in the strong effect of salinity on cod in our model. During low salinity conditions cod eggs float deeper in the water column increasing the spatial overlap with sprat thus adding to the direct mortality caused by low salinity via low oxygen conditions (Köster and Möllmann 2000a). Additionally the second feedback mechanism is partly dependent on the hydrographic situation, as *P. acuspes* is critically

dependent on the salinity level as well (Möllmann et al. 2003). Bearing in mind that negative feedback mechanisms (no matter how small) may still have disproportionately large effects in maintaining and stabilizing dynamic regimes (Scheffer et al. 2001), we found only a slow and gradual increase in cod SSB in response to bio-manipulation. On the contrary, when exposed to reductions in cod F or increasing salinity levels, the cod stock responded drastically by increasing above ecologically safe levels. Further, when studying the relative effects of changes in cod and sprat F, increasing sprat F had no additional positive effect on cod recovery.

Besides being inefficient as demonstrated by our model simulations, artificially reducing the sprat stock to low levels bears a number of ecological risks. Sprat is a so-called “wasp-waist” species in the Baltic Sea and as such largely determines the flux of energy from lower to higher-trophic levels of the food-web (Bakun 2006). Although sprat may pose a negative feedback effect on cod recruitment by preying on early life-stages, it certainly is a key food item for cod (Sparholt 1994). By drastically reducing the availability of prey for cod, food limitation and cannibalism (Neuenfeldt and Köster 2000) may prove yet another bottleneck in the ontogeny of cod. Though decreased intra-specific competition may create a favorable size distribution of sprat for juvenile cod (Van Leeuwen et al. 2008), heavy size-selective exploitation especially on larger sized sprat could potentially counteract this effect. The compensatory increase in herring SSB observed when released from sprat competition may only be of benefit for food availability of older cod age-classes, preying predominately on the larger sized herring. In addition, given no improvement in hydrographic conditions and the spread of bottom anoxia, the availability of benthic food (mainly *Saduria entomon*) may neither substitute for the loss of pelagic food supplies.

Furthermore, a lesson can be learned from the series of regime shifts occurring in the Black Sea (Daskalov et al. 2007). As predatory fish resources were depleted in the mid-1970s, a flourishing fishery for small-pelagic species such as sprat developed, boosted by higher-productivity, i.e., eutrophication and temperature driven recruitment success. Due to a massive build-up in fishing power in the early 1980s, the pelagic fish populations later collapsed, only to be replaced by gelatinous carnivores (i.e., *Mnemiopsis leydii*) in the early 1990s (Shiganova et al. 2001, Oguz and Gilbert 2007). A similar outbreak of invasive ctenophores also occurred in the Benguela upwelling system (Bakun and Weeks 2006) and was recently documented for the Baltic Sea as well (Kube et al 2007). Within the last years, these ctenophores have spread as far north as the Bothnian Sea

(Lehtiniemi et al. 2007). By feeding intensively on early life-stages of commercially important fish species such as cod and sprat it may have the potential to alter the entire Baltic Sea ecosystem (Haslob et al. 2007). Thus, we should carefully assess the ecological risks and consequences of biomanipulation, as removing sprat, the main competitor for zooplankton; we could open up a niche for invasive species and fundamentally impact future fisheries production in the Baltic Sea

Another factor which is important to consider when evaluating the effect of a sprat biomanipulation on the ecosystem is eutrophication. In the Baltic Sea, eutrophication has profoundly impacted the structure and functioning of the entire ecosystem and is considered a main factor regulating the dynamics of the fish community (Hansson et al. 2007). Concerning Eastern Baltic cod, the shift from a largely oligotrophic to a eutrophic state in the early 1950s may initially have enhanced production while lately affecting recruitment negatively through increased hypoxia in bottom waters (Österblom et al. 2007). Hansson et al. (1998) have shown that unless superseded by reductions in nutrient loadings both externally from the catchment area and internally from sediments, biomanipulation in lakes are largely ineffective. Thus, if ever performed in the whole Baltic Sea, a basin-scale biomanipulation program should indeed be superseded by massive efforts to reduce nutrient loadings, not only airborne (HELCOM, 2005a) and waterborne (HELCOM, 2005b) but also internally from leaking sediments. Concerning modeling, at least scenarios integrating biomanipulation with changing nutrient conditions in the Baltic Sea should be performed prior to an actual manipulation.

#### *4.2 Conclusions*

Emerging from our simplified MSE is the notion that doing nothing is indeed worse than doing something; hence a very reasonable incentive for action. Biomanipulation has proven an effective tool in combating eutrophication and restoring top-predator regulation in shallow lakes. However, Conley et al. (2009) and Hansson (2008) argue that any engineering method (e.g., Stigebrand and Gustafsson 2007) including biomanipulation, applied in the open Baltic Sea is likely to be neither ecologically effective nor cost effective. Especially if not cod fishing, as well as nutrient input are reduced considerably. Based on simulations from our coupled ecological-bio-economic model, we reinforce the notion by Hansson (2008) that an ocean-scale biomanipulation with the main focus of reinstating the dominance of Eastern Baltic cod may likely be (i) ecologically ineffective, (ii) operationally difficult and (iii) economically not the preferable management approach. However,

before actually implemented on a vast pan-Baltic Sea scale, we should question whether insights from bio-manipulations are indeed transferable from lakes when scaled-up to large open marine ecosystems such as the Baltic Sea. Concern should arise not primarily due to greater complexity and spatial extent but to difficulties in controlling and confining experimental manipulations in ecosystems strongly impacted by external factors, abiotic (e.g., fishing and climate variability) as well as biotic (e.g., drift and migrations of highly mobile species such as sprat; Aro 1989). We therefore urge for a careful evaluation of the bio-manipulation management approach in the Baltic Sea using not only one but several models with a varying degree of complexity in species-, spatial- and temporal resolution. Based on our modeling study, we argue reducing cod F to ecologically sound levels is the most appealing management alternative in promoting a recovery and sustainable fishery for Eastern Baltic cod.

## **5. Acknowledgements**

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## **Regime shifts, Resilience and Recovery of a Cod stock**

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### *Abstract*

In the North and Baltic Seas cod stocks collapsed as part or one of the major factors inducing large-scale ecosystem regime shifts. The relative contribution of overfishing and climate variability in causing these shifts has proven difficult to disentangle. While facing similar climatic conditions, the Sound (i.e., an area situated in the interface between the North and Baltic Seas) differs from its neighbouring areas in terms of the magnitude of fishing due to a local trawl fishing ban since 1932. By means of three independent multivariate analyses we here investigate the state and development of the Sound ecosystem, specifically testing for the occurrence of regime shifts and their potential drivers. By comparing the ecosystem development of the Sound with the neighbouring North and Baltic Seas, we were able to demonstrate the positive effect of the trawl fishing ban on the resilience of the local cod stock to environmental change. The recovery and healthy conditions of the Sound cod stock illustrates the need for adaptive marine management strategies maximizing ecosystem resilience.

## INTRODUCTION

Global fish production is under threat from overexploitation and climate change (Jackson et al. 2001, Hutchings & Reynolds 2004, Brander 2007). Besides causing an elevated risk of stock collapse (i.e., due to direct depletion by the fisheries), prolonged overfishing reduces the age, size, and geographic diversity of fish populations, thereby increasing their vulnerability to climate-driven recruitment stress (Brander 2005, Ottersen et al. 2006, Anderson et al. 2008). In order to achieve sustainability, adaptive marine management strategies that maximize ecosystem resilience (i.e., the ability to withstand and buffer against change; Holling 1973) are needed (Folke et al. 2004, Steele et al. 2004). The consequences of degrading resilience and increasing ecosystem vulnerability is clearly shown by the poor state of the Atlantic cod (*Gadus morhua*), once among the commercially most important fish species in the North Atlantic. Due to the joint effects of overfishing (Myers et al. 1997, Frank et al. 2005) and climate driven declines in productivity (Beaugrand et al. 2003) many of the stocks collapsed without showing signs of recovery (Hutchings & Reynolds 2004).

In several areas of the North Atlantic the collapse of cod stocks was part of or one of the major factors inducing large-scale reorganization of ecosystems (Frank et al. 2005, Kirby et al. 2009, Möllmann et al. 2009). These regime shifts are often driven by external forcing, including climate variability, overfishing and eutrophication (Collie et al. 2004). The relative importance of these drivers in causing regime shifts is difficult to disentangle due to co-occurring and often synergistic effects. Being able to separate these effects is of vital importance in developing ecosystem-based management strategies and achieving sustainable use of fisheries resources in the future (Pikitch et al. 2004, Marasco et al. 2007, Lindegren et al. 2009).

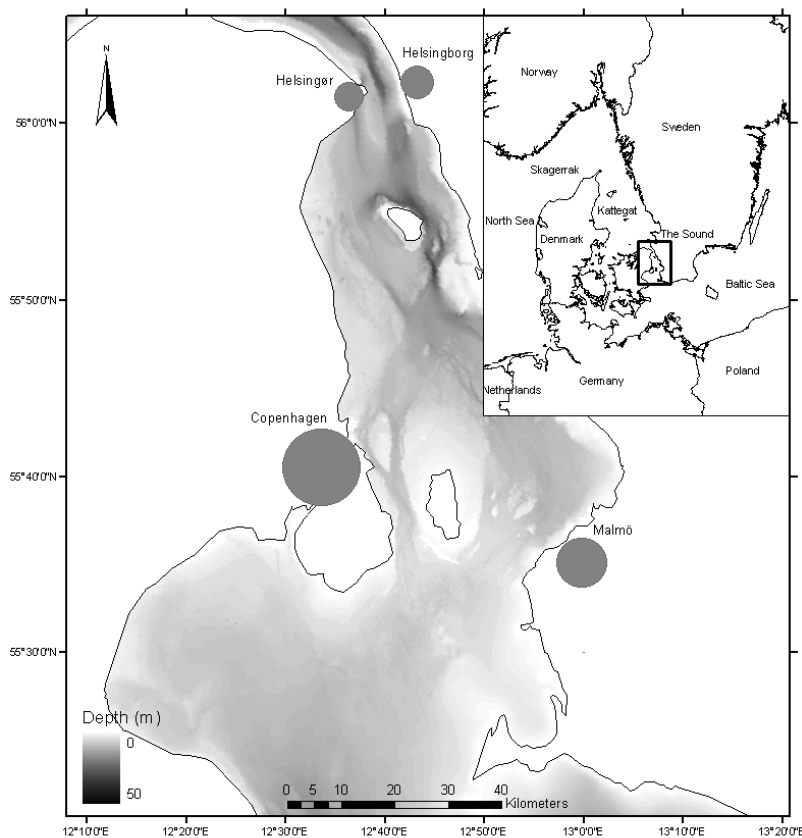
In concert with large-scale patterns of ecosystem change across the North Atlantic (Bundy et al. 2009, Drinkwater et al. 2009, Link et al. 2009), simultaneous regime shifts (during the late 1980s) have been demonstrated for the North and Baltic Seas (e.g., Beaugrand 2004, Alheit et al. 2005, Weijerman et al. 2005, Kenny et al. 2009, Möllmann et al. 2009). Both regime shifts were to a large degree triggered by climatic changes and overfishing with the collapse of the cod stocks being a strong component of these ecosystem reorganizations. In

the Baltic Sea the latter resulted in a pronounced trophic cascade leading to changes in the lower trophic levels (Osterblom et al. 2007, Casini et al. 2008, Möllmann et al. 2008).

The Sound is a narrow strait situated in the interface between the North and Baltic Seas (Fig. 1). Though being hydrologically connected to the Baltic Sea by the northward flow of brackish surface water and to the North Sea by the southward flow of high-saline bottom water, it shows marked differences in biotic conditions. These differences are manifested by locally spawning sub-populations of gadoids and flatfish (Svedäng et al. 2004), similar to sedentary coastal populations found throughout the North Atlantic (e.g., Godø 1995, Robichaud & Rose 2004). Although a spill-over effect and an exchange with adjacent populations has not been quantified, the local cod population seems largely self-sustaining (Svedäng et al. 2004), as suggested by demographic differences (Svedäng et al. 2002), genetic studies (Nielsen et al. 2005) and tagging experiments (Pihl & Ulmestrand 1988, 1993), pointing towards reproductive isolation through spawning site fidelity and/or juvenile retention (Robichaud & Rose 2004, Nielsen et al. 2005). In contrast to the depleted state of neighbouring North and Baltic Sea cod stocks, the Sound fish stocks in general and the cod stock in particular are healthy not only in stock sizes but in the age-size structure of the populations (Svedäng et al. 2002), a difference attributed to the absence of trawling activities (i.e., as trawl fishing was banned in 1932 to facilitate shipping; Svedäng et al. 2004). Hence while facing similar climatic conditions the Sound differs from its neighbouring areas in terms of the magnitude of fishing pressure on the local fish stocks. An investigation of the ecosystem development in the Sound during the last decades and a comparison with the neighbouring North and Baltic Seas may hence enable disentangling the importance of the different drivers underlying regime shifts and fish stock collapses in marine ecosystems.

Based on a large multivariate data set we investigated the state and development of the Sound, specifically testing for the occurrence of regime shifts, trophic cascades and their potential drivers. By comparing the ecosystem development in the Sound with the neighbouring North and Baltic Seas (i.e., through comparable methods across areas, Megrey et al. 2009) we were able to demonstrate the positive effect of the trawl fishing ban

on the resilience of the fish stocks and in particular the local cod population to environmental change.



**Fig. 1.** Map over the study area, the Sound (i.e., ICES Subdivision 23) and its position between the North and Baltic Seas.

## MATERIAL AND METHODS

**Data collection.** A data inventory was performed on available time series characterising the Sound ecosystem and its abiotic environment. Selection of variables was based on their ecological importance, the length of the time series and the completeness of the dataset. Furthermore, data collection was restricted to the Sound, excluding the larger Western Baltic/Kattegat area, due to: (1) data availability, (2) lack of comparable integrated ecosystem analysis in these areas, (3) a primary interest in studying an area with a limited fishery impact. In total, 74 biotic and abiotic time series from 1970 to 2006 were compiled. Due to cross-correlations between variables and missing values at the beginning of the investigated period, 48 datasets were used for subsequent analyses (Table 1), covering a period from 1979-2005.

In order to reflect the abiotic environment, variables representing both physical oceanographic and nutrient conditions were assembled. Spring and summer values of temperature and salinity were included, thus covering the main seasons for primary and secondary production as well as the relevant periods for fish reproduction. Due to a strong and permanent stratification, both surface and bottom values were used. Total annual inflow (southward) and outflow (northward) of water through the Sound, i.e., accounting for only a fraction of the total water flux between the North and Baltic Seas (Fischer & Matthäus 1996), were included to represent the hydrodynamics of the area. Furthermore, the Baltic Sea Index (BSI) was included which reflects the impact of climate variability on oceanographic processes in the area (Lehmann et al. 2002). Oxygen conditions were represented by bottom concentrations during spring and nutrient conditions by winter concentrations of nitrate, ammonium, silica and total phosphorous.

The selected biotic variables cover all trophic levels from primary producers to top-predatory fish. Summer chlorophyll *a* was used as a proxy for total phytoplankton biomass. To account for changes in the relative taxonomic composition of the phytoplankton groups during spring and summer, biomass of diatoms, dinoflagellates, cryptophyceans, nanoplankton and cyanobacteria (summer) were used in the analysis. The zooplankton community is represented by summer biomass values of copepods (*Acartia* spp., *Centropages* spp., *Pseudocalanus* spp. and *Temora longicornis*) and cladocerans (*Evadne* spp., *Oithona similis*, *Podon* spp. and *Bosmina* spp.). Benthos is characterised by annual biomass averages of molluscs, polychaetes, echinoderms and crustaceans. Annual landings from the local gill-net fishery of the commercially most important fish species cod (*Gadus morhua*), whiting (*Merlangius merlangus*), herring (*Clupea harengus*), plaice (*Pleuronectes platessa*), flounder (*Platichthys flesus*) and dab (*Limanda limanda*) were chosen to characterize the fish community. Landings of seasonally occurring species such as garfish (*Belone belone*), mackerel (*Scomber scombrus*) and eel (*Anguilla anguilla*) were excluded. However, herring landings consisting of both a local population and the Rügen spring spawning herring were included since it resides in the Sound during a major part of the year from August to March (Nielsen et al. 2001).

Environmental and biological data were extracted from published reports and the databases hosted by The Danish National Environmental Research Institute (<http://www.dmu.dk>) and the Swedish Meteorological Institute (<http://www.smhi.se>). Fish survey data were extracted from International Council for the Exploration of the Sea (ICES) database (<http://www.ices.dk>) and commercial landings from The Danish Directorate of Fisheries (<http://www.fd.dk>) and the Swedish Board of Fisheries (<http://www.fiskeriverket.se>).

**Regime shift analysis.** Principal Component Analysis (PCA) was used to extract the most important modes of variability in the time series. Beforehand, we replaced missing values in the dataset by variable averages. To improve linearity between variables and to reduce the relationship between the mean and the variance, all biological variables were  $\ln(x+1)$  transformed. Our analyses included a PCA using all 48 time series, followed by two separate PCAs for either abiotic (16 series) or biotic variables (32 series). All three PCAs were conducted based on the correlation matrix and the first factorial plane was visualised as a correlation biplot.

To identify potential regimes in the datasets Chronological Clustering was performed to objectively identify the years where the largest shifts occurred. This method describes discontinuities in a multivariate series of samples, taking into account the sequence of sampling and making it possible to eliminate singletons (Legendre et al. 1985, Legendre & Legendre 1998). To show the most important breakpoints in the dataset, the significance level  $\alpha$ , which can be considered as clustering intensity parameter, was set to 0.01 and the connectedness level to 50%. Corresponding to the methodological approach used in the PCA, data were first standardised and then the Euclidean distance function was calculated to determine the similarity between years.

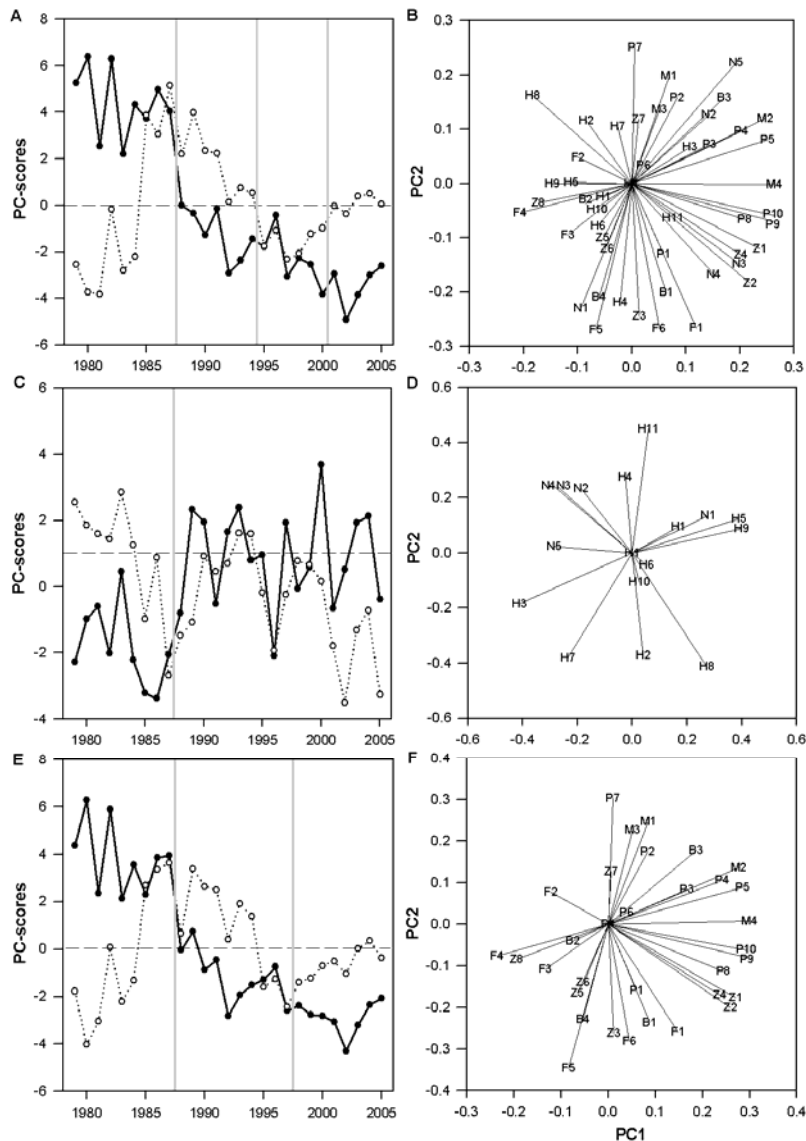
In a further analysis we applied the Sequential Regime Shift Detection Method (STARS) (Rodionov 2004) to normalized averages (e.g., Hare & Mantua 2000) of hydrographic and nutrient time series as well as for each functional group, i.e., phytoplankton, zooplankton, benthos and fish separately. The STARS algorithm is designed to detect statistically significant shifts in the mean level and the magnitude of fluctuations in time series by using modified two-sided Student's t-tests. STARS can detect shifts at different time scales and



magnitudes by varying the probability level of the tests and the cut-off length controlling the duration of regimes (Rodionov & Overland 2005). In this study we applied a significance-level of  $p=0.05$  and a cut-off length of 10 years. More information on the STARS method and Excel add-in software is available online at [www.beringclimate.noaa.gov](http://www.beringclimate.noaa.gov).

**Trophic cascade analysis.** Trophic cascades are defined by alternating top-down and bottom-up regulation and the propagation of indirect positive feedbacks between non-adjacent trophic levels (Pace et al. 1999, Casini et al. 2008). In order to provide a first understanding of the underlying processes of ecosystem regulation in the Sound we investigated the potential occurrence of trophic cascades by applying simple linear regression analysis on selected time series representing key components of the different trophic levels of the ecosystem. In addition, a regression analysis on aggregated biomasses for each trophic level was performed. All time-series were log-transformed to stabilize the variance. Model diagnostics were applied to test for the assumption of normality and independence of residuals.

**Cross-ecosystem comparisons.** For the cross-ecosystem comparison, PC1 scores from regime shift studies in the North Sea (Weijermann et al. 2005) and the Central Baltic Sea (Möllumann et al. 2009) were collected (i.e., chosen in order to cover the whole period from 1979-2005). PC1 can be considered as an integrated indicator of ecosystem state and development (Möllumann et al. 2009). The STARS method was then applied to the PC1 scores, including the Sound, to compare the timing and magnitude of the regime shifts. We also compared the spawning stock biomass (SSB), i.e., derived from standard stock assessments in the North Sea and Baltic Sea, and landings of the cod and the dominating pelagic fish stock between areas. Since landings may not accurately reflect the true stock dynamics in the Sound, we additionally collected independent survey data and CPUE estimates (landings/trawling hour) available for cod from 1991-2006 and 1996-2006 respectively. All statistical analysis were conducted using the Brodgar ([www.brodgar.com](http://www.brodgar.com)) and R software ([www.r-project.org](http://www.r-project.org)).



**Fig. 2.** Year scores at the first two axes PC1 (solid) and PC2 (dotted) resulting from the Principle Component Analysis of (A) the full dataset, (C) the abiotic data set and (E) the biotic dataset. Vertical lines indicate the time of the most important breakpoints obtained from chronological clustering using an alpha value of 0.01. Additionally, correlation biplots from each normalised PCA are presented (B, D, F). The angles between eigenvectors represent the degree of correlation between variables (see Table 1) and PC axes.

## RESULTS

**Ecosystem analysis.** The PCA of the full dataset, taking into account both abiotic and biotic variables, resulted in 35.6 % explained variance on the first two PCs. (A plot of eigenvalues for each principle component of the three PCAs is available as supplementary material in ‘Supplement 1’ at [www.int-res.com/articles/](http://www.int-res.com/articles/)). Scores along the first PC (24.2%) showed a clear temporal trend from positive values in the early years and negative values from the 1990s onwards separated by a sharp decrease in scores between 1987-1988 (Fig. 2A). The variable loadings, i.e., the length and orientation of vectors on the correlation biplot visualize the degree of correlation with the respective PC (Fig. 2B). Thus, nutrients (N2, N5), small-sized phytoplankton (P4, P5, P8, P9), cyanobacteria (P10), copepods (Z1,

Z2, Z4), microzooplankton (M4) and molluscs (B3) were mainly positively correlated to PC1, while flatfish (F2-F4), *Bosmina* spp. (Z8) and summer bottom temperatures (H8) showed negative correlations. The negative correlation thus indicates an increasing trend in each of these variables within the last 15 years, e.g., higher flatfish landings. The second PC (11.4 %) showed an initial sharp increase in scores followed by a gradual decrease and a rather stable period in the last 10 years. Large-sized phytoplankton (P2, P7) and microzooplankton (M1, M3) showed positive correlations to this axis, while landings of herring (F6), cod (F5), whiting (F1) and biomass of *Pseudocalanus* spp. (Z3) were negatively correlated with PC2. This means that these variables generally increased since the mid-1990s. Finally, note that outflow (H10) and inflow (H11) did not explain much of the variation on the first two PCs (Fig. 2B), indicating that transport and advection, no matter how important for the physical environment (Fig. 2C), seem to be rather uncorrelated to the temporal dynamics of most ecosystem components.

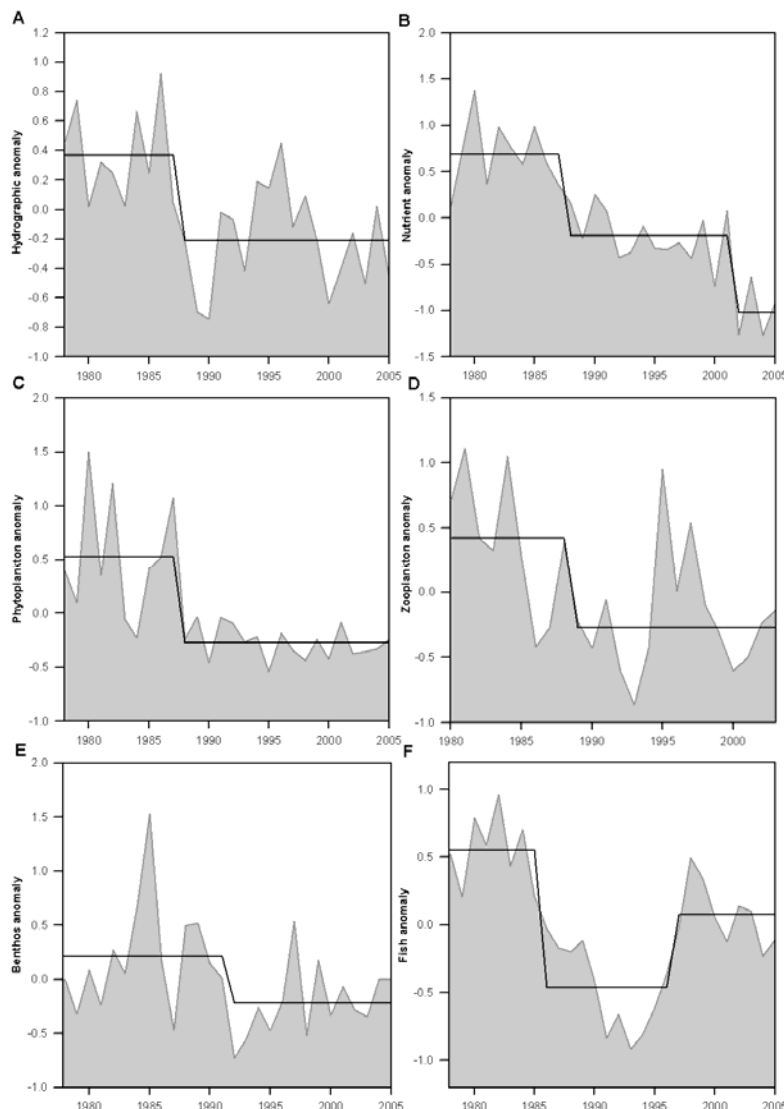
The second PCA, using only abiotic time series explained 39.2 % of the variance on the first factorial plane. PC1 scores (21.5%) showed strong fluctuations with an overall increasing trend since the late 1980s (Fig. 2C). In the correlation biplot (Fig. 2D), BSI (H9) and spring surface temperature (H5) were positively correlated to PC1, indicating their overall increase during the last decades. Contrastingly, spring bottom salinity (H3) and nutrient conditions (N2-5) decreased and showed negative correlations to the first axis. PC2 scores (17.7 %) oscillated with high values at the beginning and low values at the end of the investigated period. Volume inflow (H11) and summer bottom salinity (H4) showed positive correlations, while bottom temperatures (H7, H8) and surface salinity (H2) showed negative correlations to PC2.

The third PCA using only biological time series explained 41.3 % of the variance on the first factorial plane. The temporal development of PC1 and PC2 scores (Fig. 2E) were relatively similar to the results of the first PCA using the full dataset (Fig. 2A). During the first years PC1 scores (28.3 %) showed positive values but shifted to negative values following a sharp decrease in 1987-1988 (Fig. 2E). The eigenvectors (Fig. 2F) of small-sized phytoplankton (P4, P5, P9), cyanobacteria (P10), microzooplankton (M2, M4), copepods (Z1, Z2, Z4) and molluscs (B3) were positively correlated to PC1, while landings

of flatfish (F3, F4) and biomass of *Bosmina* spp. (Z8) showed negative correlations. PC2 scores (13.1 %) showed an increasing trend until 1991, followed by a gradual decrease and a more stable period with negative values in recent years. Dinoflagellates (P7), diatoms (P2) and microzooplankton (M1, M3) showed positive correlations to this axis, while landings of herring (F6), cod (F5), whiting (F1) and biomass of *Pseudocalanus* spp. (Z3) were negatively correlated, thus indicating comparatively high values during the last 10 years.

The vertical lines superimposed on the PCA-plots (Fig. 2) show the most important breakpoints identified by chronological clustering using an alpha value of 0.01. In all three datasets, i.e., the full- (Fig. 2A), abiotic- (Fig. 2C) and biotic dataset (Fig. 2E) respectively, a significant breakpoints was detected in 1987-1988. Furthermore, two breakpoints were identified in the full dataset in 1994-1995 and 2000-2001 (Fig. 2A) and in the biotic dataset in 1997-1998.

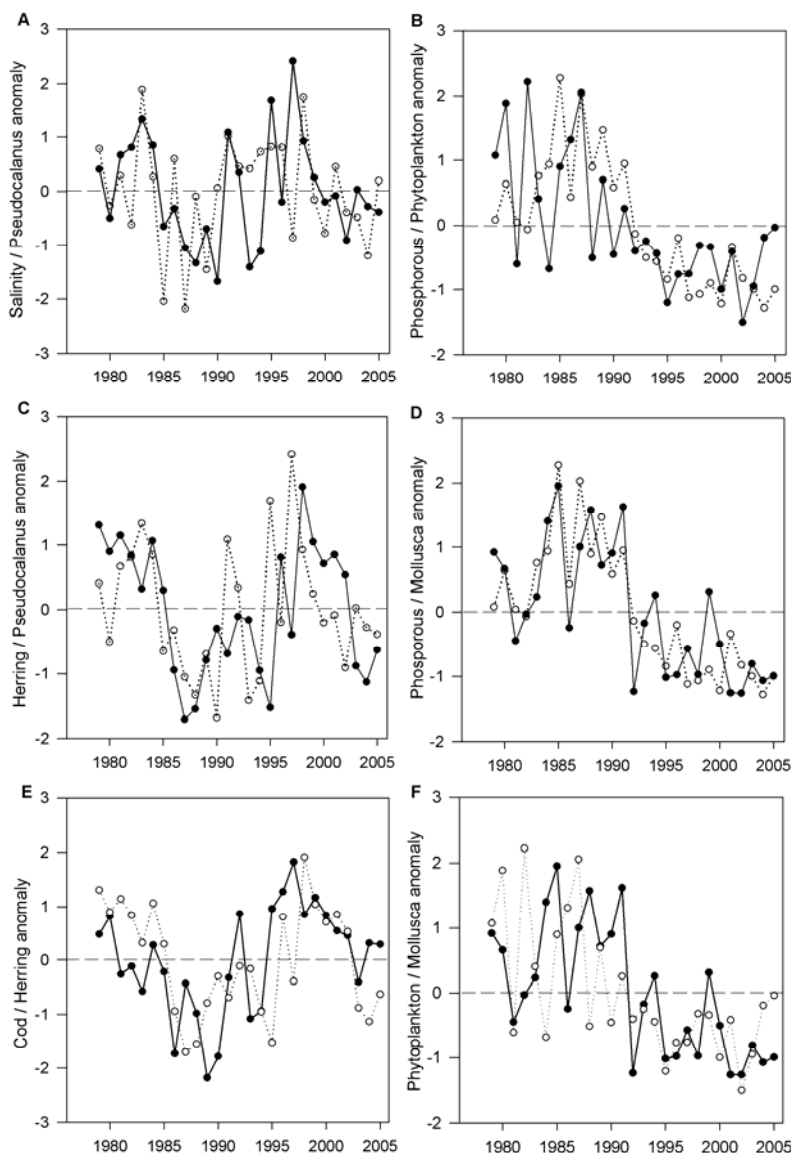
The STARS method identified significant regime shifts largely coinciding with the breakpoints detected by chronological clustering. The hydrographic data (Fig. 3A) showed a clear regime shift in 1987-1988, corresponding to a dramatic shift mainly in bottom salinity, SST and BSI. The increase and decrease in the mid-1990 were not identified as separate states. Due to a sharp decrease in nitrogen and phosphorous, the nutrient data (Fig. 3B) showed two regime shifts in 1987-1988 and 2001-2002 respectively. Coinciding with the decrease in nutrients, primary producers (Fig. 3C) also demonstrated a shift in 1987-1988. Zooplankton showed a regime shift in 1988-1989, thus lagged with one year compared to the 1987-1988 regime shifts. The sharp increase in 1994-1995 and the consecutive period of high values were due to its short duration not identified as a separate regime (Fig. 3D). Benthos data (Fig. 3E) showed one significant shift in 1991-1992, thus being delayed in comparison to the previously mentioned groups. As in all other groups, the fish data showed a sharp decrease since the mid-1980s (Fig. 3F). Though showing two consecutive declines in 1985-1987 and 1989-1991 respectively, only the first shift was found to be significant. Additionally, an opposite shift was observed in 1996-1997, possibly following the sharp decrease in the hydrography and increase in zooplankton variables in 1994-1995.



**Fig. 3.** Stepwise regime shifts in climate, nutrient and biological time-series (variables of each group are standardized to zero mean, unit variance and reverted such that the step show the same sign in all time series). (A) Climate, (B) Nutrient, (C) Primary producers, (D) Zooplankton, (E) Benthos, (F) Fish. Significant shifts in means (black solid lines) were detected using significance level,  $p = 0.05$  and a cut-off length of 10 years.

**Trophic cascade analysis.** In order to visualise top-down and bottom-up regulation in the Sound, selected time series from each functional group were graphically displayed as standardised anomalies (Fig. 4). Based on the similarities in temporal dynamics of the selected variables, the analysis suggests two parallel pathways of bottom-up regulation in the Sound, the first linking hydrographic-climatic processes to zooplankton and fish and the second linking nutrient dynamics to primary producers and benthos. The first pathway is clearly visible in the relationships between bottom salinity, *Pseudocalanus* spp., herring and cod (Fig. 4A, C, E). The variables were chosen as they represent key hydrographic variables and the dominant zooplankton and fish species in the area. The second pathway is visualised by the similar temporal dynamics of winter concentration of phosphorous, (i.e., considered the limiting nutrient in the area; Wasmund & Uhlig, 2003), total photosynthetic

biomass and mollusc biomass, the latter representing the most abundant benthic group in the Sound. A regression analysis on the selected time series showed highly significant and positive relationship between each trophic level (Table 2), i.e., between zooplankton (*Pseudocalanus* spp), planktivorous (herring) and piscivorous fish (cod) as well as between primary producers and benthos (Molluscs). Furthermore, these pattern are consistent when considering also aggregated biomasses for each trophic level (Supplement 2). This indicates strong bottom-up regulation in all parts of the ecosystem and rules out the possibility of trophic cascades, since trophic cascades are generally identified by inverse (negative) relationships between adjacent trophic levels (Pauly et al. 1998, Worm & Myers 2003, Casini et al. 2008).



**Fig. 4.** Plots of normalized time series from each trophic level, demonstrating two pathways of ecosystem regulation in the Sound. (A) Summer bottom salinity (dotted) and summer biomass of *Pseudocalanus* spp. (solid) (B) Winter total [P] (dotted) and total phytoplankton biomass (solid). (C) Summer biomass of *Pseudocalanus* spp. (dotted) and landings of herring (solid). (D) Winter total [P] (dotted) and biomass of Molluscs (solid). (E) Landings of herring (dotted) and cod (solid). (F) Summer total phytoplankton biomass (dotted) and biomass of Molluscs (solid). (A regression analysis of the presented time-series is presented in Table 2).

**Table 2.** Results of linear regression analysis on selected time series. Following the two suggested pathways of regulation, the analysis is divided into a hydrographic-climatic section (A) and a nutrient section (B). Model significance via p-values (P), degrees of freedom (df) and regression coefficients, the intercept (a) and the slope (b) with associated significance levels (\*, \*\*, \*\*\*) are indicated. In order to emphasize the type of linear relationship, a positive (+) and negative (-) sign is indicated. Finally, the coefficient of determination is shown in percent.

A. Hydrographic - Climatic pathway

Response	Predictor	d.f	P	a	b	Sign	R <sup>2</sup>
<i>Pseudocalanus</i> spp.	Herring	24	<0.001	-6.3***	0.50***	+	52
<i>Pseudocalanus</i> spp.	Cod	24	0.007	-7.1*	0.58**	+	23
Herring	Cod	24	<0.001	0.03	1.04***	+	37

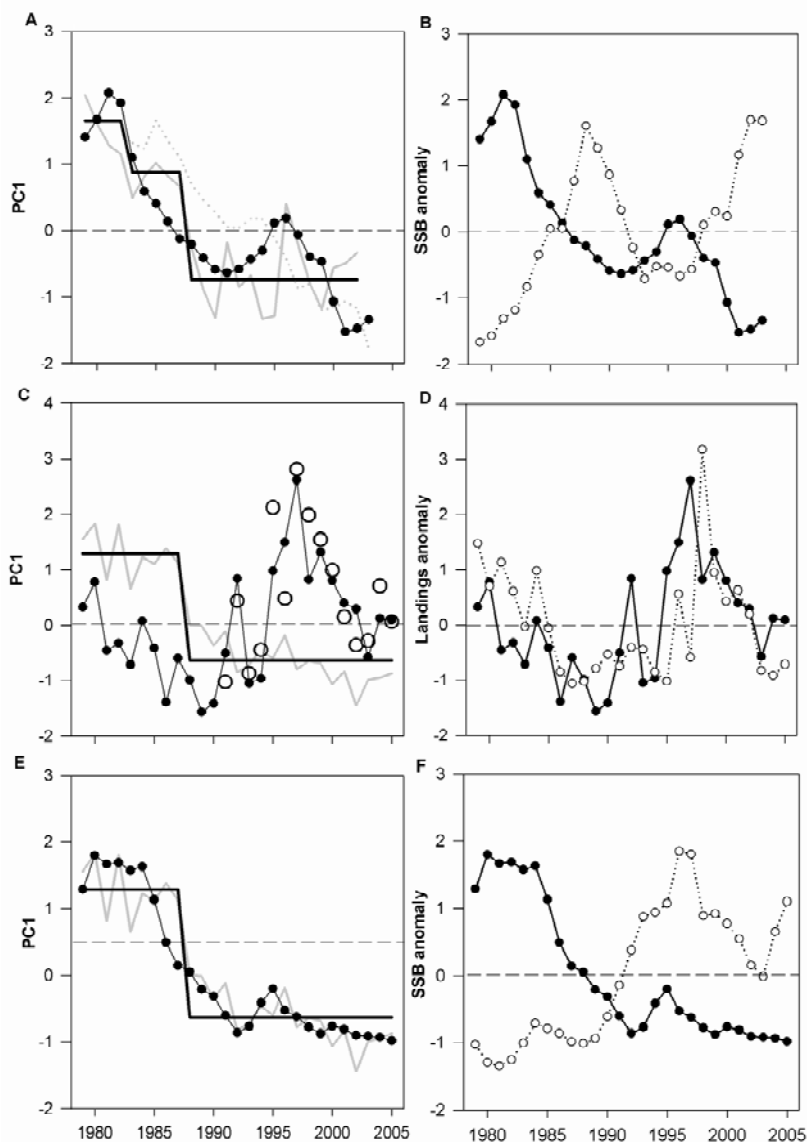
B. Nutrient pathway

Response	Predictor	d.f	P	a	b	Sign	R <sup>2</sup>
Total Phytoplankton	TP	24	<0.001	7.1*	9.3***	+	40
Mollusca	TP	25	<0.001	-3.2***	4.0**	+	62
Total Phytoplankton	Mollusca	24	0.008	16.3***	1.4**	+	22

**Cross-ecosystem comparisons.** As illustrated by the generally declining PC1 scores from the North Sea (Fig. 5A), the Sound (Fig. 5C) and the Central Baltic Sea (Fig. 5E), the areas show similar ecosystem dynamics during the observed period. Likewise, the timing and magnitude of regime shifts detected by STARS all coincide in the years 1987-1988. The cod stock dynamics from the North Sea (Fig. 5B) and Central Baltic Sea (Fig. 5F) largely follow the ecosystem developments, while for the Sound cod stock the initial decrease is followed by an increase since the mid-1990s (Fig. 5C). Since landings data may not adequately describe the cod stock dynamics, we additionally plotted landings data with independent survey data available from 1991-2006. The strong correlation with survey data ( $r = 0.79$ ,  $p < 0.001$ ) as well as with CPUE estimates (i.e., landings/trawling hour;  $r = 0.82$ ,  $p < 0.001$ ) indicated that landings may reflect the true stock dynamics, at least from the early 1990s onwards.

In the North and Baltic Seas, the regime shift and collapse of the cod stocks triggered a trophic cascade causing changes in the lower trophic levels (Österblom et al. 2007, Casini et al. 2008, Möllmann et al. 2008, Kirby et al. 2009). The trophic cascade is illustrated by

the strong negative correlation between cod and sprat ( $r = -0.72$ ,  $p < 0.001$ ), the dominating planktivorous species in the Baltic Sea (Fig. 5F) and between cod and herring ( $r = -0.81$ ,  $p < 0.001$ ), one of the main planktivorous fish species in the North Sea (Fig. 5B). As opposed to the neighbouring areas, the positive relationship between the Sound cod and herring (Table 2) suggests no trophic cascade, instead a strong bottom-up regulation in the area.



**Fig. 5.** Comparison of PC1 scores (grey), SSB of cod (solid) and pelagic fish species (dotted) from the North Sea (a, b), the Sound (c, d) and the Central Baltic Sea (e, f). Herring is shown for the North Sea and the Sound, while sprat is shown for the Central Baltic Sea. (Additionally, PC1 scores (dotted) from Kenny et al. (2009) are shown for the North Sea). Solid black lines represent the regime shifts as detected by the STARS method. Cod landings from the Sound are compared with normalized survey data available from 1991-2006 (circles).

## DISCUSSION

In the North Sea and Central Baltic Sea the cod stocks collapsed simultaneously to large-scale ecosystem reorganisations (Reid et al. 2003, Beaugrand 2004, Weijerman et al. 2005, Casini et al. 2008, Möllmann et al. 2008). These regime shifts are considered driven by the combined and synergistic effects of both overfishing and climate variability (Weijerman et



al. 2005, Möllmann et al. 2009). Despite the absence of commercial trawl-fishing, we also demonstrate a clear shift in the Sound ecosystem. Given the coherent patterns and synchronous timing of regime shifts across the entire North Atlantic (Bundy et al. 2009, Drinkwater et al. 2009, Link et al. 2009), atmospheric-oceanographic changes are the most likely driver. In the North and Baltic Seas, regional climate and hydrographic conditions are mainly influenced by large-scale circulation patterns causing periodic inflow events from the North Atlantic (Hänninen et al. 2000, Reid et al. 2003). These events have been shown to affect all parts of the ecosystems from lower trophic levels (Reid et al. 1998, Möllmann et al. 2000, Beaugrand et al. 2003, Wasmund & Uhlig 2003) to higher trophic levels (Kröncke et al. 1998, Möllmann et al. 2003, Durant et al. 2004) and involve a suite of different physical and biological processes, mainly related to effects of temperature, salinity, oxygen, turbulence and advection (Ottersen et al. 2001). In the mid-1980s, the NAO and BSI shifted sharply from a negative to a positive phase, giving rise to anomalous temperatures, salinities and oxygen conditions throughout the whole area. These climate anomalies by means of direct and indirect biological feedbacks most likely induced the simultaneous regime shift observed in the North Sea, Central Baltic Sea and the Sound in 1987-1988.

Depending on the internal structure and the type of external forcing, ecosystem regime shifts may be discriminated into three qualitatively different types: smooth, abrupt, and discontinuous (Collie et al. 2004). While the first two represent generally reversible transitions between alternative ecosystem states, a discontinuous shift involves hysteresis, a process preventing the system from switching back to the previous state even if external conditions are restored (Scheffer et al. 2001). In the North and Baltic Seas, the regime shift and collapse of the cod stock resulted in a pronounced trophic cascade leading to changes in the lower trophic levels (Österblom et al. 2007, Casini et al. 2008, Möllmann et al. 2008, Kirby et al. 2009). This internal restructuring of the food-web may presently maintain the ecosystem in its currently less desirable ecosystem state by means of negative feedbacks (Bakun 2006, Casini et al. 2009, Möllmann et al. 2009). While the North and Baltic Sea regime shifts may be described as discontinuous, the Sound regime shift shows no signs of trophic cascade or shift in trophic control (i.e., between top-down and bottom-up regulation) and is therefore likely of the abrupt but still reversible kind. Given similar

external physical forcing, the observed difference between regime shifts in the North Sea, Baltic Sea and the Sound are likely due to a different magnitude of anthropogenic influences, e.g., with respect to eutrophication and fishing pressure, which both affect the internal structure and resilience of the ecosystem.

Eutrophication has caused regime shifts in lakes (Carpenter et al. 1987, Scheffer & van Nes 2007) and estuarine ecosystems (Daskalov 2007, Hansson et al. 2007, Oguz & Gilbert 2007, Österblom et al. 2007). The Sound faced severe eutrophication in the early 1980s, however due to the implementation of efficient waste water treatment, river run-off (mainly of phosphate) was markedly reduced (The Sound Water Cooperation 2004). In combination with limited inflow of nutrient-rich bottom water from the North Sea, the nutrient reductions likely caused the strong decline in nutrient conditions during the period. Furthermore, Wasmund & Uhlig (2003) related decreasing trends in cyanobacteria and chlorophyll *a* to increasing temperatures and a decrease in nutrient loadings, in particular to phosphorous which is considered a co-limiting nutrient in this area (HELCOM 2002). The shift from small-sized phytoplankton species and N-fixing cyanobacteria to larger-sized diatoms and dinoflagellates in the early 1990s may be explained by a combination of climate and nutrient forcing (Wasmund & Uhlig 2003, Henriksen 2009).

Henriksen et al. (2001) showed significant positive response of macrobenthos abundances to winter nutrient input and spring primary production in Danish waters. Likewise, Kröncke et al. (1998) showed a similar effect on macrozoobenthos in the North Sea. Decreasing nutrient loadings and primary production in combination with a milder climate probably induced the observed changes in the benthic community in the Sound, especially the drastic decrease of filter-feeding molluscs. (Note that the changes may not be attributed to fishing activities, as towed bottom-fishing gear, i.e., trawls has been banned since 1932). The invasion of the alien species, *Marenzelleria neglecta* may further explain the shift in dominance to polychaetes in the early 1990s (Strömberg & Persson 2005).

Overfishing by reducing the mean age, mean size, and geographic diversity of populations has been shown to increase the sensitivity of fish stocks to climate-driven recruitment stress (Brander 2005, Ottersen et al. 2006, Anderson et al. 2008), thereby impairing their

resilience to withstand and buffer against environmental change (Folke et al. 2004). For the North Sea cod, recruitment stress is primarily caused by temperature driven mismatch in prey availability reducing the survival of young cod (Beaugrand et al. 2003), while for Baltic cod, low salinity and oxygen concentrations directly impair recruitment through egg and larvae mortalities (Köster et al. 2005). Furthermore, the large sprat stock may impose key negative feedbacks by preying on cod eggs (Köster & Möllmann 2000) and reducing the main food source of cod larvae (i.e., the copepod *Pseudocalanus acuspes*) (Möllmann & Köster 2002). Though mechanisms are not investigated in detail, our study suggests a positive effect of both bottom salinity and zooplankton availability (i.e., through *Pseudocalanus* spp.) on cod recruitment in the Sound.

Following the regime shift and collapse of the North Sea and Baltic Sea cod stocks, the populations remained at historically low levels with no or only weak signs of recovery (i.e., a slight increase in Eastern Baltic cod has been observed during the recent years). In contrast, the Sound fish stocks in general and the local cod population in particular shows a clear recovery in the mid-1990s after the regime shift. The resilience and recovery potential of the Sound cod stock is likely due to the absence of commercial trawl fishing, as only local gill-net fisheries are allowed to operate in the area (Svedäng et al. 2004). As a consequence, the cod stock shows demographic conditions in terms of age- and size-distribution far better than the overexploited neighbouring stocks (Svedäng et al. 2002, Supplement 3). With many large, old and experienced individuals and several generations contributing to spawning (Ottersen et al. 2006, Anderson et al. 2008), the Sound cod stock seem more resilient to recruitment stress and could therefore recover following years of potentially unfavourable climate conditions for spawning. Whether the trawling ban itself offers increased resilience to the ecosystem by protecting important benthic habitats and organisms, vital for growth and recruitment of demersal fish species such as cod (Collie et al. 2000), is presently unclear. To that end, we stress the need for further investigations on the local fish stocks in general and the cod population in particular, in order to provide detailed understanding of the mechanisms underlying fish stock resilience in the Sound.

## Conclusions

Ecosystems worldwide have already shown clear evidence of change in response to climate change (Walther et al. 2002, Rosenzweig et al. 2008) and even more pronounced alterations might be encountered in the future, especially as climate scenarios predict drastic changes in atmospheric-oceanographic forcing (IPCC 2007). Resilient ecosystems are able to absorb extreme events without changing fundamentally, but if the resilience is weakened it can be restored only slowly (Folke et al. 2004). Furthermore, hysteresis may even prevent the ecosystem from switching back to the previous state as it is not sufficient to restore external conditions (Scheffer et al. 2001). External conditions can be only partly influenced (e.g., by reducing nutrient loads) but we are indeed able to control fisheries through appropriate and ecologically sound management actions. While the regime shifts in the North and Baltic Seas may involve hysteresis, and as such be described as discontinuous, the Sound regime shift shows no signs of trophic cascade or hysteresis and may therefore be of the abrupt but still reversible kind. The current study indicates that low fishing pressure and hence healthy fish population sizes and structures can obviously change the response of an ecosystem to external forcing. The Sound cod stock recovered to pre-shift conditions whereas neighbouring areas remained in a depleted state. The socio-economic costs of an ecosystem switch with a decline of commercially valuable fish species can be enormous and therefore the maintenance and restoration of ecosystem resilience is an important part of a successful ecosystem-based fisheries management strategy (Folke et al. 2004, Marasco et al. 2007).

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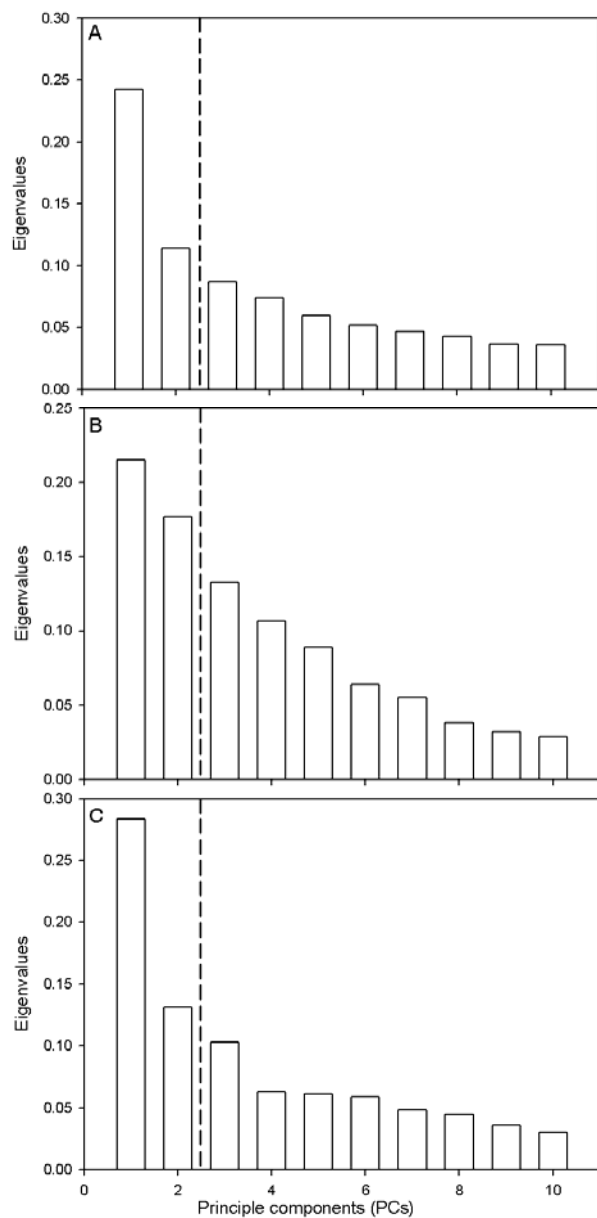
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**Table 1.** Description of time series used in multivariate analysis.

Variable	Abbreviation	Season	Unit	Source
Surface salinity	H1	Spring	psu	DMU/SMHI
Surface salinity	H2	Summer	psu	DMU/SMHI
Bottom salinity	H3	Spring	psu	DMU/SMHI
Bottom salinity	H4	Summer	psu	DMU/SMHI
Surface temperature	H5	Spring	°C	DMU/SMHI
Surface temperature	H6	Summer	°C	DMU/SMHI
Bottom temperature	H7	Spring	°C	DMU/SMHI
Bottom temperature	H8	Summer	°C	DMU/SMHI
Baltic Sea Index	H9	Winter		IFM
Volume Outflow	H10	Annual	km <sup>3</sup>	SMHI
Volume Inflow	H11	Annual	km <sup>3</sup>	SMHI
Bottom oxygen	N1	Spring	ml l <sup>-1</sup>	DMU/SMHI
Nitrate	N2	Winter	µmol l <sup>-1</sup>	DMU/SMHI
Ammonium	N3	Winter	µmol l <sup>-1</sup>	DMU/SMHI
Silica	N4	Winter	µmol l <sup>-1</sup>	DMU/SMHI
Total phosphorous	N5	Winter	µmol l <sup>-1</sup>	DMU/SMHI
Chl. a	P1	Summer	µg l <sup>-1</sup>	DMU
Diatoms	P2	Spring	µgC l <sup>-1</sup>	DMU
Dinoflagellates	P3	Spring	µgC l <sup>-1</sup>	DMU
Cryptophyceans	P4	Spring	µgC l <sup>-1</sup>	DMU
Nanoplankton	P5	Spring	µgC l <sup>-1</sup>	DMU
Diatoms	P6	Summer	µgC l <sup>-1</sup>	DMU
Dinoflagellates	P7	Summer	µgC l <sup>-1</sup>	DMU
Cryptophyceans	P8	Summer	µgC l <sup>-1</sup>	DMU
Nanoplankton	P9	Summer	µgC l <sup>-1</sup>	DMU
Cyanobacteria	P10	Summer	µgC l <sup>-1</sup>	DMU
Flagellates (microzooplankton)	M1	Spring	µgC l <sup>-1</sup>	DMU
Other microzooplankton	M2	Spring	µgC l <sup>-1</sup>	DMU
Flagellates (microzooplankton)	M3	Summer	µgC l <sup>-1</sup>	DMU
Other microzooplankton	M4	Summer	µgC l <sup>-1</sup>	DMU
<i>Acartia</i> spp.	Z1	Summer	µgC l <sup>-1</sup>	DMU
<i>Centropages</i> spp.	Z2	Summer	µgC l <sup>-1</sup>	DMU
<i>Pseudocalanus</i> spp.	Z3	Summer	µgC l <sup>-1</sup>	DMU
<i>Temora longicornis</i>	Z4	Summer	µgC l <sup>-1</sup>	DMU
<i>Evadne</i> spp.	Z5	Summer	µgC l <sup>-1</sup>	DMU
<i>Oithona similis</i>	Z6	Summer	µgC l <sup>-1</sup>	DMU
<i>Podon</i> spp.	Z7	Summer	µgC l <sup>-1</sup>	DMU
<i>Bosmina</i> spp.	Z8	Summer	µgC l <sup>-1</sup>	DMU
Crustacea	B1	Annual	g m <sup>-2</sup>	DMU
Echinoderm	B2	Annual	g m <sup>-2</sup>	DMU
Mollusca	B3	Annual	g m <sup>-2</sup>	DMU
Polychaeta	B4	Annual	g m <sup>-2</sup>	DMU
Whiting landings	F1	Annual	t year <sup>-1</sup>	FD
Dab landings	F2	Annual	t year <sup>-1</sup>	FD
Plaice landings	F3	Annual	t year <sup>-1</sup>	FD
Flounder landings	F4	Annual	t year <sup>-1</sup>	FD
Cod landings	F5	Annual	t year <sup>-1</sup>	FD
Herring landings	F6	Annual	t year <sup>-1</sup>	FD

\* For a more detailed description and data requests, please contact the ICES/HELCOM Working Group on Integrated Assessments of the Baltic Sea (WGIAB) or the corresponding author.

## Supplement 1



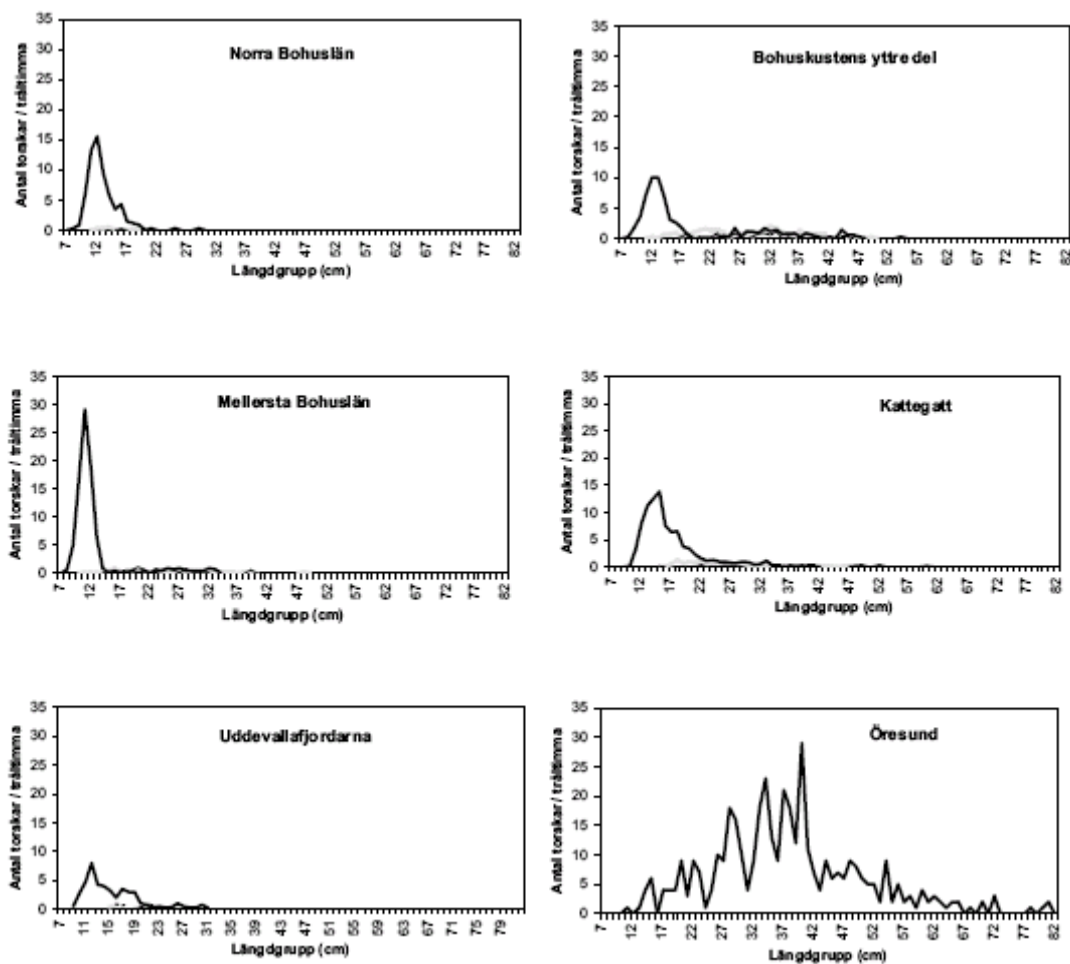
**Supplementary figure 1.** A scree plot of eigenvalues for each separate PCA, i.e., the full- (A), abiotic- (B) and biotic analysis (C). The dotted vertical lines indicate the first factorial plane (i.e., PC1 and PC2) represented on the corresponding correlation biplots.

**Supplement 2**


**Supplementary table.** Results of linear regression analysis on aggregated biomasses for each trophic level (functional group) respectively.

Response	Predictor	d.f	P	a	b	Sign	R <sup>2</sup>
Zooplankton	Climate	25	0.03	2.3***	0.34*	+	14
Pelagic fish	Zooplankton	24	<0.001	11.3***	1.5***	+	46
Demersal fish	Pelagic fish	25	0.04	11.6***	0.2*	+	13
Phytoplankton	Nutrients	25	<0.001	19.8**	5.2***	+	46
Benthos	Phytoplankton	23	0.02	3.3***	0.05*	+	17

### Supplement 3



**Supplementary figure 2.** Mean size-distribution of cod (numbers/haul hour) in different areas along the Swedish west coast during 2001. The Sound is shown in the lower right panel. (From Svedäng et al. 2002).



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